A REVIEW OF DROMAEOSAURID SYSTEMATICS AND PARAVIAN PHYLOGENY

ALAN H. TURNER

Department of Anatomical Sciences
Stony Brook University
Stony Brook, New York 11794-8081
and
Division of Paleontology
American Museum of Natural History

PETER J. MAKOVICKY

Department of Geology
The Field Museum
1400 South Lake Shore Drive
Chicago, Illinois 60605-2496

MARK A. NORELL

Division of Paleontology
American Museum of Natural History

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ABSTRACT

Coelurosauria is the most diverse clade of theropod dinosaurs. Much of this diversity is present in Paraves—the clade of dinosaurs containing dromaeosaurids, troodontids, and avialans. Paraves has over 160 million years of evolutionary history that continues to the present day. The clade represents the most diverse living tetrapod group (there are over 9000 extant species of Aves—a word used here as synonomous with "bird"), and it is at the root of the paravian radiation, when dromaeosaurids, troodontids, and avialans were diverging from one another, that we find the morphology and soft tissue changes associated with the origin of modern avian flight. Within the first 15 million years of known paravian evolutionary history members of this clade exhibited a difference of nearly four orders of magnitude in body size, a value that is similar to the extreme body size disparity present today in mammalian carnivorans, avians, and varanoid squamates. In this respect, Paraves is an important case study in characterizing the patterns, processes, and dynamics of evolutionary size change. This last point is of particular interest because of the historical significance placed on the role of body size reduction in the origin of powered avian flight.

Our study reviews and revises the membership of Dromaeosauridae and provides an apomorphy-based diagnosis for all valid taxa. Of the currently 31 named dromaeosaurid species, we found 26 to be valid. We provide the most detailed and comprehensive phylogenetic analysis of paravians to date in order to explore the phylogenetic history of dromaeosaurid taxa. The general pattern of paravian relationships is explored within the broader context of Coelurosauria with an emphasis on sampling basal avialans, because of their importance for character optimizations at the base of Paraves.

A large dataset was constructed by merging two datasets, one examining coelurosaur relationships broadly (based on previous TWiG datasets) and the other examining avialan relationships specifically (Clarke et al., 2006). This merged dataset was then significantly revised and supplemented with novel character analysis focusing on paravian taxa. During character analysis, particular attention was given to basal members of Dromaeosauridae, enigmatic basal paravians such as *Jinfengopteryx elegans* and *Anchiornis huxleyi*, and the incorporation of new morphological information from two undescribed troodontid species from the Late Cretaceous of Mongolia. A final dataset of 474 characters scored for 111 taxa was used to address paravian evolution. This dataset is important in that it bridges a phylogenetic gap that had persisted between studies on birds and studies on all other coelurosaurs. Most scorings in this matrix were based on the direct observation of specimens.

All most parsimonious trees recovered in the cladistic analysis support the monophyly of Paraves, Troodontidae, Dromaeosauridae, and Deinonychosauria. A new clade of basal troodontids is discovered including two undescribed Mongolian troodontids and *Jinfengopteryx elegans*. *Xiaotingia* and *Anchiornis* form a clade at the base of Troodontidae. Recently proposed relationships within Dromaeosauridae are further supported and a succession of clades from Gondwana and Asia form sister taxa to a clade of Laurasian dromaeosaurids. Avialan monophyly is strongly supported with *Archaeopteryx*, *Sapeornis*, *Jeholornis*, and *Jixiangornis* forming the successive sister taxa to the *Confuciusornis* node. This topology supports a more basal position for *Sapeornis* than previous phylogenetic analyses and indicates a progressive acquisition of a fully "avian" shoulder morphology.

INTRODUCTION

Rationale

Dromaeosaurid remains are rare. Yet in the past several years we have seen an increase in dromaeosaurid diversity and geographic extent. Even the distribution and evolution of complex featherlike integumentary structures (Allain and Taquet, 2000; Makovicky et al., 2005; Norell and Xu, 2005; Norell et al., 2006; Turner et al., 2007a; Longrich and Currie, 2009) is now well understood in the clade. Numerous species-level taxa have been described, including several fragmentary forms that are ambiguously dromaeosaurids (see in part Norell and Makovicky, 2004). Until recently the group was best known from the Upper Cretaceous of Asia and North America. In the last few years many new taxa have been discovered from the Lower and Upper Cretaceous of Asia, Europe, North America, and South

America (Norell and Makovicky, 2004; Makovicky et al., 2005; Novas et al., 2009; Longrich and Currie, 2009). Among the most intriguing of these finds are specimens from the Lower Cretaceous Yixian Formation of Liaoning, China, many of which preserve epidermal stuctures including feathers (Norell and Xu, 2005). Some of these even provide evidence of coloration (Li et al., 2010a, 2010b, 2012). Dromaeosaurids have been a focus of many studies because of their close relationship to Avialae (Gauthier, 1986; Sereno, 1997; Makovicky and Sues, 1998; Holtz, 1998; Norell et al., 2001). The primary aim of this study is to clarify the phylogenetic history of dromaeosaurid theropods as well as broader deinonychosaur and paravian relationships.

Deinonychosauria is the group of coelurosaurian theropod dinosaurs that consist of the sickle-clawed Dromaeosauridae and Troodontidae. This is generally regarded as the group most closely related to birds. Chinese, Mongolian, and South American dromaeosaurids and Chinese and Mongolian troodontids display an interesting mosaic of derived and primitive characters that raise issues concerning dromaeosaurid phylogeny, the relationships of these taxa to other deinonychosaurs and birds, and even the monophyly of Deinonychosauria (Norell et al., 2006).

With the rapid increase in dromaeosaurid diversity, many of the historically diagnostic characters of Dromaeosauridae become smeared farther down the coelurosaur tree or resorted, so they arise convergently. The same is true for many so-called "avian" or avialan features. As basal members of Dromaeosauridae and Troodontidae have been described many of these features have been reinterpreted at a more general level as paravian synapomorphies. Moreover, the fact that most detailed avialan phylogenetic studies have been conducted outside the context of a species-level coelurosaur dataset (Chiappe and Calvo, 1994; Chiappe, 1995; Norell and Clarke, 2001; Clarke and Norell, 2002; Clarke, 2004; Clarke et al., 2006) complicates a clear understanding of the character changes occurring across the nonavialan/avialan transition. These studies present detailed and repeatedly corroborated hypotheses of avialan evolution but do not provide the more comprehensive framework required to explore three of the main questions we seek to answer through rigorous tests of: (1) the sister-group status of Deinonychosauria to Avialae, (2) the monophyly of Deinonychosauria in the context of newly described basal troodontids, dromaeosaurids, and avialans, and (3) the placement of *Rahonavis ostromi*, which was considered a basal avialan but later shown to be a basal dromaeosaurid (Makovicky et al., 2005).

Providing answers to these questions is critical. The presence of filamentous integumentary structures (Xu et al., 1999, 2000, 2001; Ji et al., 2001) and feathers of modern aspect in some dromaeosaurids (Norell et al., 2002; Norell and Xu, 2005), an avianlike sleeping posture in the basal troodontid *Mei long* (Xu and Norell, 2004), the troodontid affinities of the feathered *Jinfengopteryx* (Turner et al., 2007b), and the small body size of many basal paravians underscore the avianlike features of deinonychosaurs and indicate that characteristic "bird" morphology and behavior evolved in nonavialan dinosaurs prior to the origin of powered flight. It is, therefore, important that investigations of characters associated with flight origins within dinosaurs be based, not on speculative scenarios, but on testable hypotheses of character optimization that our phylogeny allows.

As of this writing, the number of dromaeosaurid taxa continues to increase almost weekly. Most of these specimens are found in incredibly rich northern Chinese rocks referred to collectively as the Jehol Group, but continued work in other localities has led to the discovery of additional dromaeosaurids in Djadokhta Formation and equivalent deposits in Inner Mongolia (Xu et al., 2010) and in undersampled regions in southeastern Europe (Csiki et al., 2010). As a result of this, and the ever-expanding toolkit for exploring theropod systematics and biology, it is impossible to provide a truly synthetic treatment of a single diverse clade like Dromaeosauridae. Nevertheless, we are as comprehensive and up-to-date as possible in this review of dromaeosaurid systematics and evolution.

Systematic Framework

Precladistic studies and their resultant classifications are hampered by plesiomorphic diagnoses or overreliance on particular

typological morphologies (e.g., the body size–related Carnosauria/Coelurosauria division within Theropoda). This resulted in an oversimplified but ambiguous taxonomy and rampant paraphyly. Application of cladistic methodology to dinosaurian taxa, beginning in the early 1980s, led to the resolution of large-scale patterns of dinosaur phylogeny (Gauthier, 1984, 1986; Sereno, 1986, 1997, 1999; Holtz, 1994, 1998, 2001; Wilson and Sereno, 1998; Makovicky and Sues, 1998; Norell et al., 2001; Makovicky et al., 2005). Since the seminal work of Gauthier (1986) that established the framework for many of the major relationships among theropod dinosaurs, subsequent authors have made important strides in clarifying fine-scale relationships among constituent lower clade levels (Russell and Dong, 1993; Forster et al., 1998; Holtz, 1998; Makovicky and Sues, 1998; Sereno, 1999).

Theropoda

Gauthier (1986) applied a stem-based definition to Theropoda, which consists of the last common ancestor of birds (Aves) and all descendents closer to birds than to sauropodomorph dinosaurs. This definition combined the traditional usage of Marsh's (1881) Theropoda with the realization that Aves (Linnaeus, 1758) was deeply nested within Theropoda as originally proposed by Thomas Huxley (1868). Gauthier (1986) also broke the Carnosauria[1] versus Coelurosauria convention for size-related classifications by specifying an explicit definition of Coelurosauria, tying it to a less inclusive clade near the avian origination within Theropoda.

Subsequent analyses to Gauthier's (1986) have rejected Carnosauria in favor of tyrannosaurids as coelurosaurs and *Allosaurus* and *Acrocanthosaurus* as more basal taxa (Holtz, 1994; Sereno, 1997). Unlike Crocodylomorpha, which has only a few large clades, showing just a few levels of gross morphological organization (i.e., "sphenosuchians," "protosuchians," Thalattosuchia, Notosuchia, Neosuchia), Theropoda is comprised of numerous "family"-level clades that form a ladderlike, pectinate organization of relationships. The monophyly of these theropod clades are well established, although among basal theropods a few large questions remain. These include ceratosaur monophyly and Coelophysoidea monophyly (Carrano et al., 2002; Carrano and Sampson, 2008; Rauhut, 2003; Smith et al., 2007).

Coelurosauria

Coelurosauria includes several clades with both small- and large-bodied taxa such as Tyrannosauroidea, Ornithomimosauria, Therizinosauria, Oviraptorosauria, Compsognathidae, Alvarezsauroidea, Dromaeosauridae, Troodontidae, and Avialae (fig. 1). Both some of the largest (*Tyrannosaurus rex*) and smallest (bumble bee hummingbird) known theropods belong to this clade. Additionally, a number of small-bodied basal taxa are known that are not readily assignable to any one of the established subclades of Coelurosauria: *Ornitholestes hermanni, Coelurus fragilis, Tugulusaurus faciles, Xinjiangovenator parvus, Tanycolagreus topwilsoni, Aniksosaurus darwini, Zuolong salleei*, and *Nqwebasaurus thawazi*. Major clade level relationships within Coelurosauria were first addressed by Gauthier (1986), Holtz (1994, 1998), Makovicky and Sues (1998), and Sereno (1997, 1999). While these analyses did much to establish the general framework of relationships among coelurosaurs it was not within a species-level framework. The study of Norell et al. (2001) was the first to analyze at the species level and corroborated much of the underlying topology found in previous supraspecific analyses. Nevertheless, the position of compsognathids and the placement of alvarezsauroids within Coelurosauria remain extremely contentious, although the discovery and description of several new taxa may ameliorate some of this uncertainty shortly.

Paraves

As coined and defined by Sereno (1997, then 1998 respectively), Paraves is a stem-based clade of derived coelurosaurs named to set apart the closest relatives of birds (Avialae) from more distinct coelurosaur

[1] In Gauthier's analysis Carnosauria was composed primarily of tyrannosaurids with a few more basal tetanurans such as *Allosaurus* and *Acrocanthosaurus*.

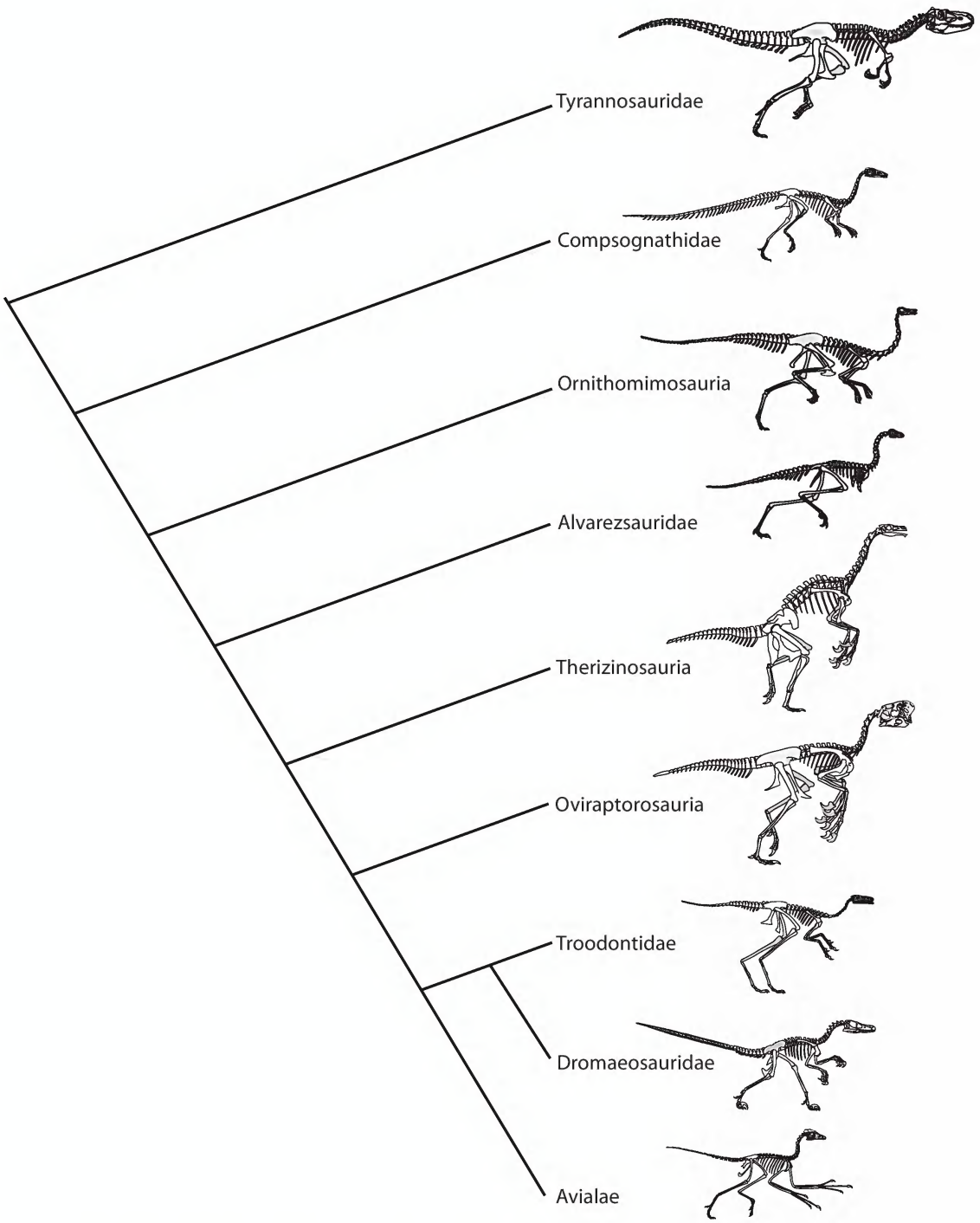


Fig. 1. Cladogram showing interrelationships of the major clades of Coelurosauria.

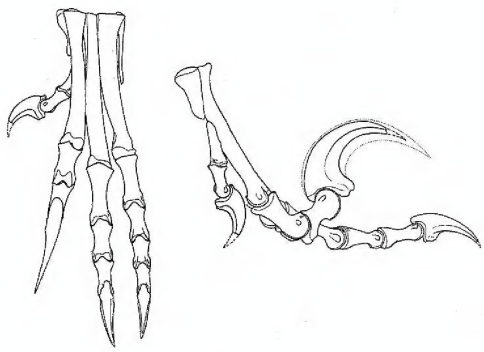


Fig. 2. Illustration of the foot of *Deinonychus antirrhopus* showing the derived pedal morphology characteristic of Deinonychosauria. Adapted from Ostrom (1969a).

relatives (i.e., *Oviraptor* and more basal taxa).[2] Dromaeosaurids, troodontids, and avialans currently constitute this clade.

Deinonychosauria was erected by Colbert and Russell (1969) to include the few dromaeosaurids then known, with the name derived from the best-known dromaeosaurid at the time, *Deinonychus*. Deinonychosaurs are characterized by a distinctive foot morphology comprised of a modified, raptorial digit II (fig. 2), exhibited in both dromaeosaurids and troodontids. Both Colbert and Russell (1969) and Ostrom (1969a) discussed the great similarity between dromaeosaurids (which were expressly included in Deinonychosauria) and the two troodontids known at the time (*Saurornithoides* and *Stenonychosaurus* (= *Troodon*)), but neither explicitly included the latter two taxa in Deinonychosauria. In Gauthier (1986) Deinonychosauria was a terminal taxon in the analysis and he explicitly discussed it in terms of including both Dromaeosauridae and Troodontidae. However, he expressed reservations about the monophyly of the clade in the addendum included at the end of the paper (Gauthier, 1986: 47). At the time that this study was undertaken, few of the relevant taxa were well described or illustrated, and access was limited.

[2]Sereno's first definition was given as "All maniraptorans closer to Neornithes than to *Oviraptor*." This has been subsequently modified by Holtz and Osmólska (2004) to have species as specifiers therefore it is now "The most inclusive clade containing *Passer domesticus* (Linnaeus 1758) but not *Oviraptor philoceratops* Osborn 1924."

Barsbold (1983a), Currie (1987), Osmólska (1981), Osmólska and Barsbold (1990), Currie and Zhao (1993), and Currie (1995) have all questioned the monophyly of Deinonychosauria. This skepticism was generally based on the argument that the modified second digit in these two taxa are morphologically dissimilar and therefore nonhomologous and that Dromaeosauridae lacked many of the derived pneumatic morphologies present in the braincase of troodontids. As a result, these studies favored a close relationship between troodontids and ornithomimosaurs. The analyses of Holtz (1994, 1998, 2001) and Senter et al. (2004) similarly did not support deinonychosaur monophyly. With the discovery of basal taxa in both Ornithomimosauria and Troodontidae it has been well established that the derived similarity between the two clades was convergently acquired as basal members in each lack those derived morphologies (Makovicky et al., 2003; Hwang et al., 2004a; and see discussion in Xu et al., 2002a). Forster et al. (1998) recovered a paraphyletic Deinonychosauria with Troodontidae the sister taxon of Avialae and Dromaeosauridae the sister taxon to that clade.

In all the cases mentioned above (except for Senter et al., 2004), Dromaeosauridae and Troodontidae were analyzed at the supraspecific level, greatly limiting the ability to reliably estimate the basal conditions in each clade and therefore reconstruct the interrelationships of the two clades. Sereno (1997, 1999) recovered a monophyletic Deinonychosauria even though Dromaeosauridae and Troodontidae were included as supraspecific composite terminal taxa. Beginning with the publication of Norell et al. (2001), all subsequent analyses employing expanded and modified versions of that dataset (Xu et al., 2002a; Makovicky et al., 2003; Xu and Norell, 2004; Makovicky et al., 2005; Norell et al., 2006; Turner et al., 2007a, 2007b) or analyzed at a species level (Senter, 2007, although not Senter et al., 2004) have recovered a monophyletic Deinonychosauria as the sister taxon of avialans (but see Xu et al., 2011).

Historically these two groups were known by only a handful of taxa and characterized by exemplar taxa like *Deinonychus antirrhopus* and *Troodon formosus*. Only recently has the diversity of dromaeosaurid and troodontid dinosaurs begun to expand and become appreciated.

Dromaeosauridae: In just the past decade, the number of described dromaeosaurids has increased from six species to more than 31. Hypotheses of a dromaeosaurid species-level phylogeny have generally been unresolved or conflicting (figs. 3, 4). Most descriptive work remains preliminary with detailed, well-illustrated descriptions provided for only a handful of taxa (Currie, 1995; Norell and Makovicky, 1997, 1999; Barsbold and Osmólska, 1999; Hwang et al., 2002; Turner et al., 2007a, 2011). Consequently, morphological variation among and between dromaeosaurid taxa is poorly understood. Adding to the issues of the underappreciation of morphological variation in this clade is the notion that the first described dromaeosaurids (*Deinonychus*, *Velociraptor*, *Dromaeosaurus*) are morphologically similar. The recently discovered small, avialanlike taxa *Microraptor zhaoianus*, *Sinornithosaurus millenii*, and *Buitreraptor gonzalezorum*, along with dromaeosaurids previously thought to be true avialans (*Unenlagia comahuensis* and *Rahonavis ostromi*) and their kin (*Austroraptor*), greatly increase the range of morphological variation within the Dromaeosauridae (Novas et al., 2009) and alter what is reconstructed as the prototypical basal conditions for dromaeosaurids.

Troodontidae: Although still less diverse taxonomically than Dromaeosauridae, a similar increase in the number of named troodontid species has occurred. Four of the basalmost taxa were described within the past decade and two undescribed Mongolian taxa represent new additions to the base of Troodontidae. The phylogeny of troodontids is better resolved and more stable than that of dromaeosaurids (Makovicky et al., 2003; Xu and Norell, 2004),[3] but this may be due to a lack of focus on this problem. *Mei long* from the lower Yixian Formation of China and *Sinornithoides youngi* from the Ejinhoro Formation of Inner Mongolia are important for being preserved in the stereotypical sleeping posture present in living birds—that posture further suggests that avianlike behavior and not just morphology occurs earlier in theropod history than the origin of birds, something that is also suggested by fossils that show brooding behavior in the oviraptorosaur *Citipati osmolskae* (Norell et al., 1995). The exact phylogenetic position of the recently described four-winged paravian *Anchiornis*, which has variably been interpreted as either an avialan or a troodontid (Xu et al., 2009) has great significance for understanding the evolution of aerial locomotion in paravians and ultimately for the origin of avian flight. Furthermore, the discovery of *Jinfengopteryx* and *Anchiornis* clearly shows that like dromaeosaurids, at least some troodontids had a complete component of feathers of modern aspect.

Avialae: Basal avialan relationships are fairly well resolved (Chiappe, 2002; Clarke, 2004; Clarke et al., 2006; You et al., 2006) (fig. 5). However, current analyses including paravian taxa usually include few avialans; often only a few exemplar taxa such as *Archaeopteryx* and *Confuciusornis*. This has resulted in spurious relationships at times (e.g., Mayr et al., 2005), poor control on which characters optimize as avialan synapomorphies, and the absence of a phylogenetic framework for inferring ancestral conditions for Avialae and in turn Paraves.

Clade Names and Taxonomic Conventions

All taxonomic systems are ultimately subjective. Traditionally, archosaur systematists have largely developed and defended the idea of ancestry-based taxonomy (e.g., phylogenetic taxonomy) (Clark, 1986; Gauthier, 1986; Gauthier and Padian, 1985; de Queiroz and Gauthier, 1990, 1992, Brochu, 1999; Brochu and Sumrall, 2001). Theropod workers in particular have been prolific in applying

[3] Although this certainly relates, at least in part, to (1) the fewer number of troodontids known, thereby enabling its inclusion in a phylogenetic analysis, and (2) the more complete nature of the troodontids included in phylogenetic analyses. A larger number of incomplete dromaeosaurids have been considered phylogenetically and the clade appears to exhibit both wider morphological disparity and wider geographic range. A focus on dromaeosaurid sampling over troodontid sampling may also relate to the excellent monograph by Ostrom (1969a), which carefully documented the morphology of *Deinonychus*. To date no such similar monograph has been produced for any troodontid, although the relatively more fragmentary taxa *Saurornithoides* and *Zanabazar* (Norell et al., 2009) have been thoroughly described.

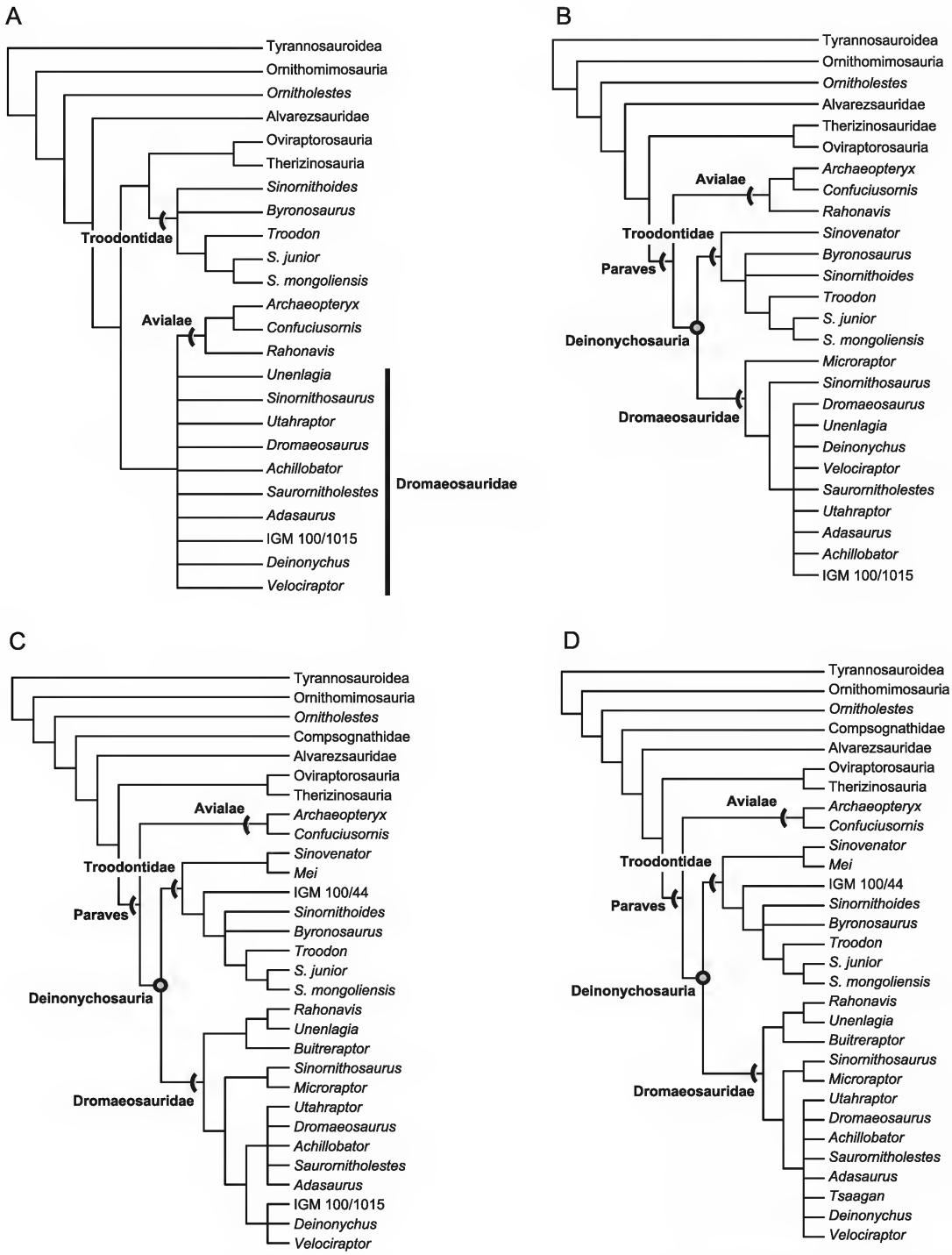


Fig. 3. Strict consensus topologies from previous versions of the Theropod Working Group (TWiG) matrix. **A,** Norell et al. (2001); **B,** Hwang et al. (2002); **C,** Makovicky et al. (2005); **D,** Norell et al. (2006).

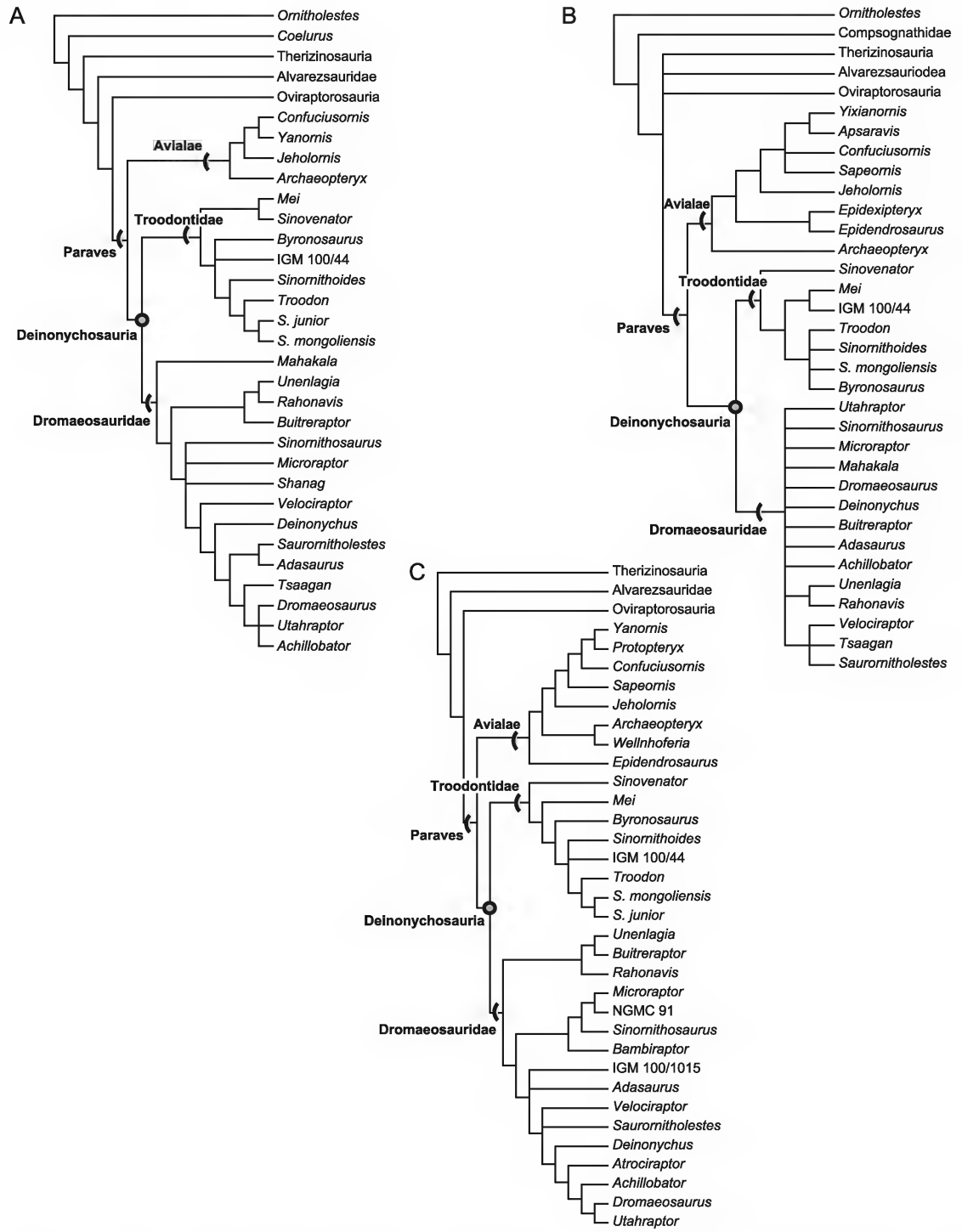


Fig. 4. Strict consensus topologies from recent phylogenetic analyses of coelurosaur relationships that used a version of the TWiG matrix as a backbone. **A,** Zanno (2010); **B,** Choiniere et al. (2010); **C,** Senter (2007).

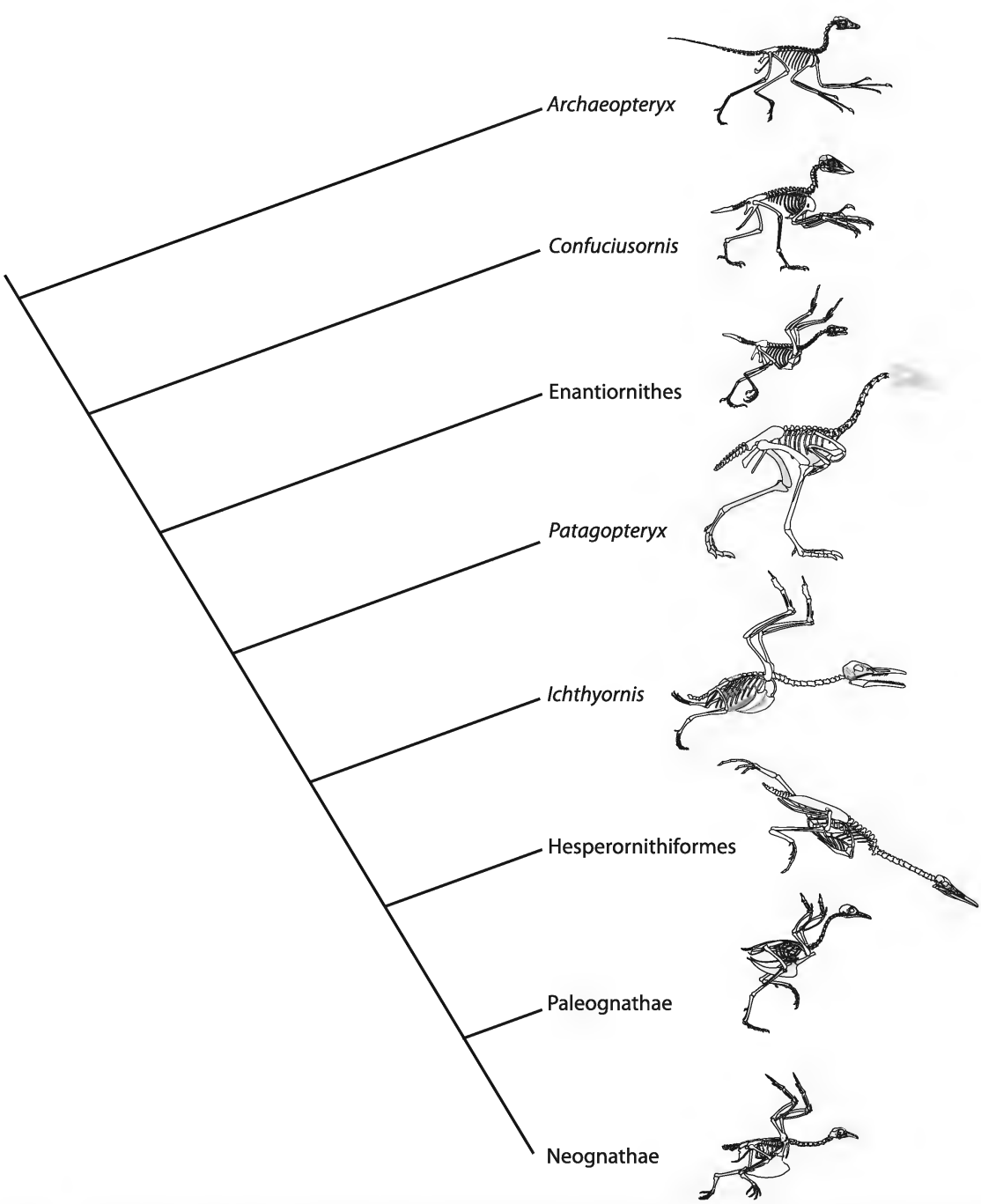


Fig. 5. Summary cladogram showing the broad pattern of relationships within Avialae. Adapted from Clarke (2004) and Chiappe (2002).

phylogenetically defined clade names to nodes in the theropod tree (see Sereno et al., 2005, for a list of clade names).

The application of a phylogenetic taxonomy remains contentious. A complete discussion of this issue would be lengthy and is certainly beyond our scope (see de Queiroz and Gauthier, 1990, 1992, 1994; Moore, 1998; Nixon and Carpenter, 2000; Benton, 2000; Brochu and Sumrall, 2001; Dyke, 2002). Although a few comprehensive taxonomic schemes have been proposed for Theropoda (Sereno, 1997,1998; Padian et al., 1997a, 1997b, 1999), changing relationships among theropod clades and an explosion of the number of known paravian taxa has resulted in new clade names and changes in the use of existing clade names. The clade names applied in the present study (fig. 6) were selected to maximize and facilitate tree discussions and conform most closely to contemporary use among basal coelurosaur and avialan workers. However, in no way are they rank based in a classical sense.

COMMENT ON THE DEFINITION OF AVES: Gauthier (1986) applied a crown-group definition to Aves, which consists of the last common ancestor of Ratiti, Tinami, and Neognathae and all of its descendants. This restricted the name Aves to the least inclusive monophyletic group containing all living birds. This definition excluded *Archaeopteryx lithographica* and numerous fossil taxa commonly referred to as "birds" from Aves. These taxa and Aves proper are subsumed by the more inclusive stem-based lineage Avialae, which Gauthier (1986) coined to encompass fossil taxa historically thought to be birds because of the presence of feathers and presumed flight abilities. However, nearly every single character that at one time was thought to make something a "bird" is now known to occur progressively earlier in theropod evolution. Therefore, "bird" is a colloquial term that lacks a meaningful taxonomic or scientific basis as it has no precise phylogenetic meaning.

Although accepted by many theropod systematists, there are some who still prefer the traditional (noncrown group) use of Aves (Sereno, 1997, 1999; Chiappe, 2002; Senter, 2007). However, crown groups reflect the notion that living taxa preserve a larger suite of characters (including behavioral and molecular data) and therefore their relationships may be more highly corroborated than fossil-only taxa (Jefferies, 1979). Additionally, crown-group definitions ensure that paleontologists and neontologists refer to the same taxon when issues in phylogeny (or those based on phylogeny such as diversity, evolutionary rate or biogeography) span the fossil record to the Recent. We find these justifications for the crown-group definition of Aves and use of Avialae compelling, and furthermore see no reason to ascribe special status to *Archaeopteryx* as the earliest member of Aves, and as such will employ the Gauthier (1986) definitions herein.

PART 1: THE DROMAEOSAURIDAE, MATTHEW AND BROWN, 1922

This section is intended to provide a detailed treatment of all taxa that have been referred to Dromaeosauridae. At times this may include descriptions of all or portions of holotype material in places where such material was not initially described, or when available descriptions were found lacking in sufficient detail. Unfortunately, we do not provide as many detailed descriptions and images of many of these taxa as we would like. These are points of focus for future work. More often this section will simply discuss and comment on dromaeosaurid species and review our current understanding of the validity of these taxa (table 1). For each taxon, the temporal and stratigraphic occurrence will be noted along with the original diagnosis provided by the author(s). This will be followed by a discussion and a revised diagnosis relying on unique combinations of characters and specific references to autapomorphies (marked by asterisks) when available for each taxon based on firsthand revision of the holotype and referred material as well as the phylogenetic analysis presented in Part 2.

ASIAN DROMAEOSAURIDS

ACHILLOBATOR GIGANTICUS PERLE ET AL., 1999

HOLOTYPE: MNUFR 15 (figs. 7, 8).

DISTRIBUTION: Cenomanian-Santonian, Late Cretaceous, Baynshiree Formation (Dornogov), Mongolia (fig. 9; table 2).

ORIGINAL DIAGNOSIS: The diagnosis for the taxon given by Perle et al. (1999) included

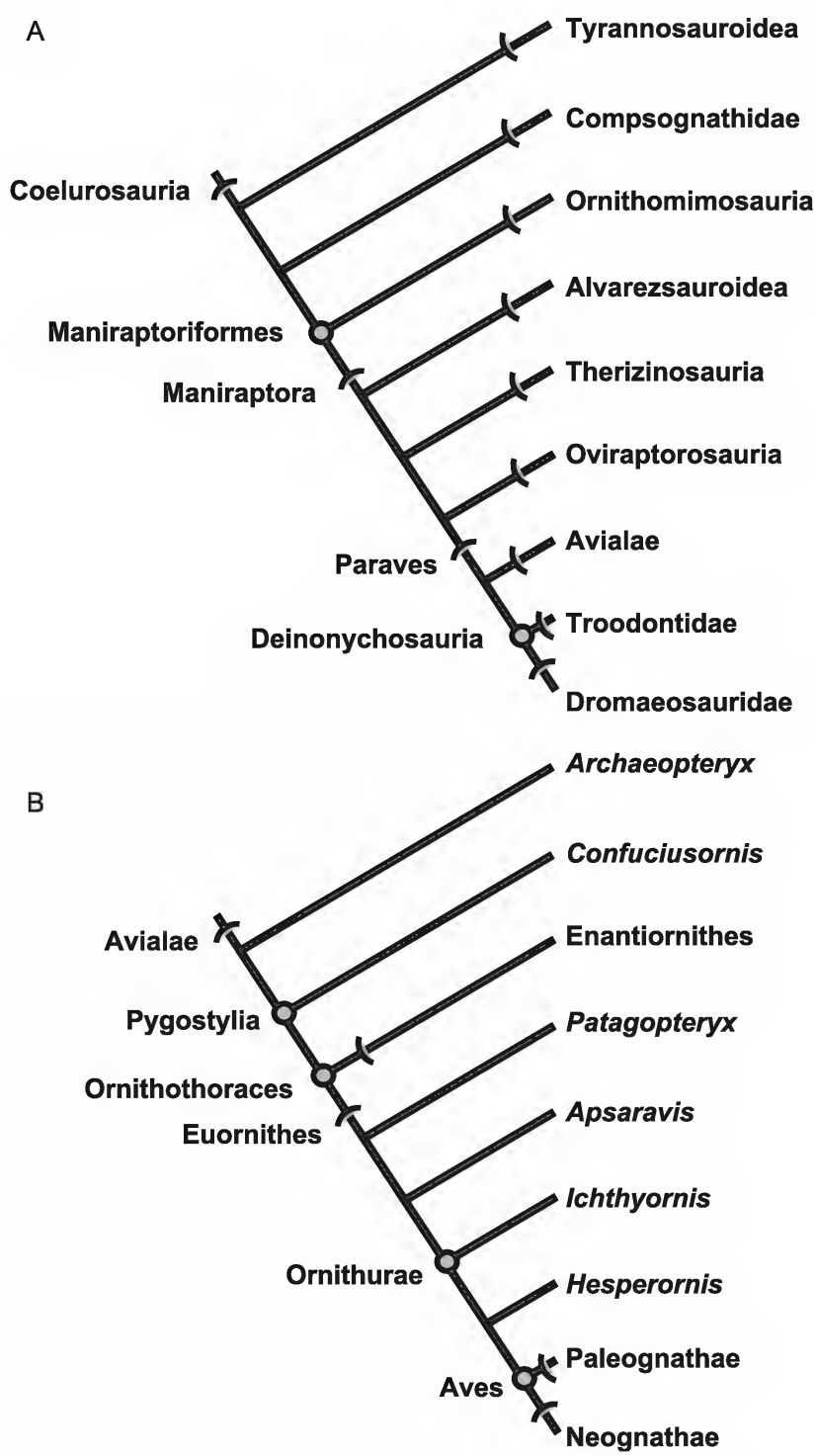


Fig. 6. Generalized cladograms showing the clade names and taxonomic conventions employed in the current study. **A,** clade names within nonavialan Coelurosauria; **B,** clade names within Avialae. Open circles denote node-based names; curves, stem-based names.

TABLE 1
Valid Species of Dromaeosauridae

Taxon	Reference
Achillobator giganitcus	Perle, Norell, and Clark, 1999
Adasaurus mongoliensis	Barsbold, 1983a
Atrociraptor marshalli	Currie and Varricchio, 2004
Austroraptor cabazai	Novas et al., 2009
Balaur bondoc	Csiki et al., 2010
Bambiraptor feinbergorum	Burnham et al., 2000
Buitreraptor gonzalezorum	Makovicky et al., 2005
Deinonychus antirrhopus	Ostrom, 1969a
Dromaeosaurus albertensis	Matthews and Brown, 1922
Graciliraptor lujiatunensis	Xu and Wang, 2004
Hesperonychus elizabethae	Longrich and Currie, 2009
Mahakala omnogovae	Turner et al., 2007b
Microraptor zhaoianus	Xu et al., 2000
Neuquenraptor argentinus	Novas and Pol, 2005
Pyroraptor olympius	Allain and Taquet, 2000
Rahonavis ostromi	Forster et al., 1998
Saurornitholestes langstoni	Sues, 1978
Shanag ashile	Turner et al., 2007a
Sinornithosaurus millenii	Xu et al., 1999
Tianyuraptor ostromi	Zheng et al., 2010
Tsaagan mangas	Norell et al., 2006
Utahraptor ostrommaysorum	Kirkland et al., 1993
Unenlagia comahuensis	Novas and Puerta, 1997
Unenlagia paynemili	Calvo et al., 2004
Velociraptor mongoliensis	Osborn, 1924b
Velociraptor osmolskae	Godefroit et al., 2008

a large number of symplesiomorphies with coelurosaurs and more derived coelurosaurian clades. Following Perle et al. (1999: 8), these included: "hindlimbs very stout, massive, and comparable short; forelimbs probably elongated as well, based on the preserved radius, pes of medium (shortened) length; penultimate and ungual phalanges of the second digit robust, particularly the proximoventral process of the penultimate phalanx; metacarpal III long and irregular with a slender shaft; skull with large semicircular to oval vertically placed antorbital fenestra, second and third accessory fenestrae oriented subvertically; 11 maxillary teeth, all teeth with anterior and posterior serrated margins; denticles on posterior margin bigger than anterior ones; cervical vertebrae short, massive and sharply angled; caudal vertebrae long and platycoelus; caudals with extremely long rodlike prezygapophyseal processes and chevrons also very much elongated into long, paired double bony rods extending forward; ischium with large triangular obturator process situated on proximal half of the ischial shaft; pubis is long, very stout with anteroposterior directed large distal expansion; in general, the pubis is propubic."

REVISED DIAGNOSIS: A large dromaeosaurid diagnosed by the following combination of characters and autapomorphies: promaxillary fenestra completely exposed; promaxillary and maxillary fenestra elongate and vertically oriented at same level in maxilla*; metatarsal III wide proximally; femur longer than tibia (estimated mass >300 kg); pelvis propubic; large triangular obturator process on ischium situated on proximal half of ischial shaft; and boot at distal symphysis of pubis both cranially and caudally developed.

DISCUSSION: This is the second largest of the described dromaeosaurid taxa with a tibial length of 490 mm (fig. 8). The taxon is based on a left maxilla, left femur and tibia, left metatarsals III and IV, right ilium, pubis,

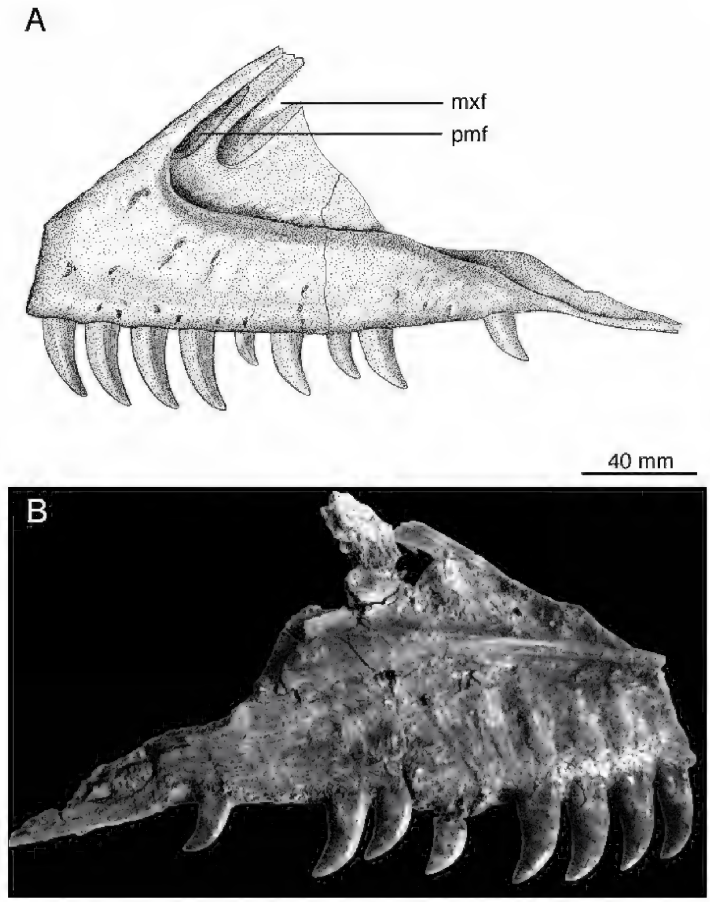


Fig. 7. Maxilla of *Achillobator giganticus* (MNUFR 15) in lateral (**A**) and medial (**B**) views.

and ischium, fragmentary teeth, several isolated caudal vertebrae, and rib fragments.

The only description of this taxon is nefarious in that it was published without the knowledge of any of the junior authors based on a preliminary draft left in Mongolia in 1997. Most of Perle et al.'s (1999) original diagnosis is uninformative and consists of plesiomorphic characteristics. "Short, stout, and massive hindlimbs" is uninformative but when more precisely stated, as "femur longer than tibia," this feature is revealed as unique with respect to other dromaeosaurids when both elements are known. Elongate forelimbs are entirely speculative based on the preserved radius, whereas the short pes and robust, modified penultimate and ungual phalanges of the second digit are more widely characteristic of deinonychosaurs (Norell and Makovicky, 2004). The cervical vertebrae are short and massive, and the articular facets are sharply angled anteriorly—a feature not unique to *Achillobator giganticus* but instead common to members of Oviraptorosauria and Paraves. Caudals with extremely long, rodlike prezygapophyses and chevrons are not diagnostic for *Achillobator giganticus*. Extremely elongate prezygapophyses and chevrons are synapomorphic for a subclade of dromaeosaurids, and as such are grounds for referring this taxon to this clade, but not to diagnose it.

The large oval-shaped and vertically oriented antorbital fenestrae are diagnostic for this taxon, whereas teeth with anterior and posterior serrated margins are present in *Dromaeosaurus albertensis*, *Atrociraptor marshalli*, and *Utahraptor ostrommaysorum*. The large triangular obturator process on the ischium is situated on the proximal half of the ischial

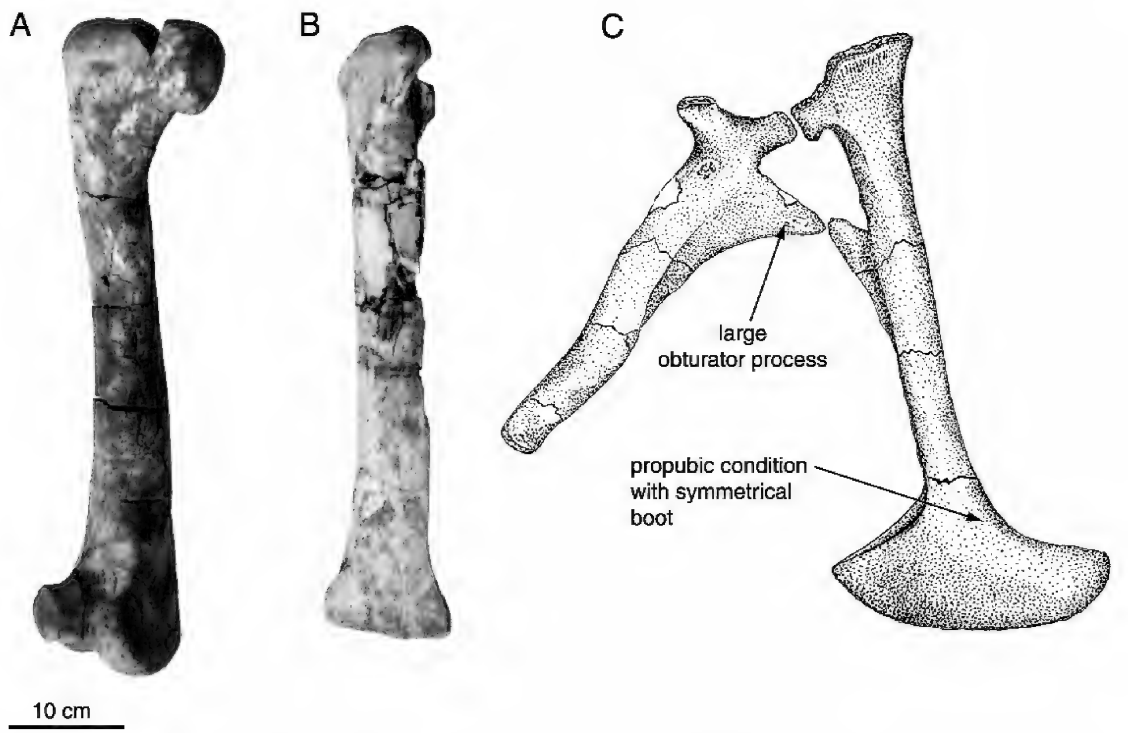


Fig. 8. Select postcranial remains of *Achillobator giganticus* (MNUFR 15). **A,** femur in posterior view; **B,** tibia in anterior view; **C,** illustration of pubis and ischium.

shaft (fig. 8). This is a reversal relative to other dromaeosaurids and in this context it is autapomorphic for *Achillobator giganticus.*

The propubic nature of the pubis and the morphology of the pubic boot are the most diagnostic characters of this taxon. The ilium is similar to *Adasaurus mongoliensis* and to a lesser extent *Velociraptor* and *Deinonychus* by having a squared-off anterior iliac process and a small flange for the m. iliotibialis. The distal symphysis of the pubis is both cranially and caudally developed into a "boot" in *Achillobator giganticus,* as is the case in *Deinonychus antirrhopus* (Norell and Makovicky, 2004).

In the phylogenetic analyses of Xu et al. (2002a), Hwang et al. (2002) and Xu and Norell (2004), *Achillobator* is recovered in a clade with *Dromaeosaurus*, or *Deinonychus* + *Dromaeosaurus* when *Adasaurus* is removed from the analysis. This clade is unambiguously supported by the presence of D-shaped premaxillary teeth and a loss of opisthopuby (Norell and Makovicky, 2004). Novas and Pol (2005) recover *Achillobator* in an unresolved clade with *Dromaeosaurus*, *Adasaurus*, and *Utahraptor* when *Saurornitholestes langstoni* is removed from the analysis. Senter et al. (2004) found *Achillobator* the sister taxon of a *Dromaeosaurus* + *Utahraptor* clade. This was based on the presence of a dorsoventrally deep jugal process on the maxilla ventral to the antorbital fenestra, posterior dorsal vertebrae with a pair of pneumatopores on each side, an obturator process that is not distally displaced, and a femur that is longer than the tibia (fig. 8). More recent analyses (Makovicky et al., 2005; Norell et al., 2006; Turner et al., 2007a, 2007b) find *Achillobator* in a clade with *Utahraptor ostrommaysorum*, *Dromaeosaurus albertensis* and sometimes *Adasaurus mongoliensis*.

It has been suggested that *Achillobator* was a chimera (Burnham et al., 2000). However, since the specimen was found in semiarticulation (A. Perle, personal commun.) and all of the elements are the same color and preservation, assignment of these elements to a single individual is justified (Norell and Makovicky, 2004). Furthermore, even though *Achillobator* is an unusual dromaeosaurid

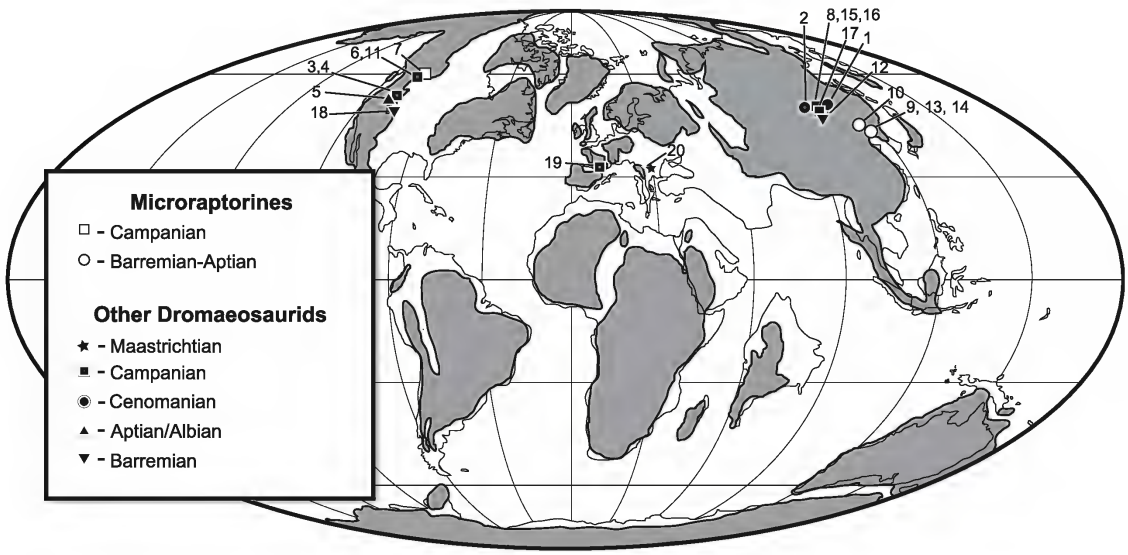


Fig. 9. Geographic distribution of Laurasian dromaeosaurids illustrated on a paleogeographic globe of the mid-Cretaceous (adapted from Smith et al., 1994).

with seemingly aberrant features it continues to be supported as a dromaeosaurid in empirical analyses (e.g., Norell and Makovicky, 2004; this study).

Adasaurus mongoliensis Barsbold, 1983

Holotype: IGM 100/20 (figs. 10–13).

Distribution: Campanian or Maastrichtian, Late Cretaceous, Nemegt Formation (Bayankhongor) of southwestern Mongolia.

Original Diagnosis: Reduced second pedal ungual.

Revised Diagnosis: A medium-sized dromaeosaurid diagnosed by the following combination of characters and autapomorphies: dorsoventrally expanded maxillary process of jugal; descending process of lacrimal strongly curved anteriorly; large surangular foramen on mandible; dorsally displaced triangular process along lateral edge of quadrate shaft*; pleurocoels only on anterior sacrals; "notched" anterior margin of preacetabular blade of ilium; and reduced pedal ungual of digit II*.

Discussion: Although partially figured and labeled as "*Adasaurus*" in a paper by Barsbold (1977), this taxon was not formally described until 1983. Barsbold (1983a) based this taxon on an incomplete skull, ischium, and pubis (IGM 100/20), as well as a partial right hindlimb including a complete pes (IGM 100/21). Barsold (1983a) refrained from giving a detailed description of this taxon, instead referring to its "great similarity...with other representatives of the [Dromaeosauridae]." The only diagnostic trait listed was the reduction of the usually enlarged, trenchant second pedal ungual to a size comparable to that of the other pedal digits. Additional references to the morphology of *Adasaurus mongoliensis* appear in Barsbold (1983b), Perle et al. (1999), and Norell and Makovicky (2004). Contrary to Norell and Makovicky (2004) the holotype of *Adasaurus mongoliensis* does not lack a skull and the pelvis is not pathological.

Currie and Varricchio (2004) reference additional cranial and postcranial material (IGM 100/22 and IGM 100/23) that remains undescribed. As it turns out, this additional material appears to represent a new taxon, a brief description of which was given in an abstract (Kubota and Barsbold, 2007). IGM 100/23 and IGM 100/22[4] are from the Shine Us Khuduk and Teel Ulaan Jalzai localities, respectively, at which the Baynshiree Formation crops out (Kubota and Barsbold, 2007).

[4]These specimens are listed by Kubota and Barsbold (2007) with the institutional abbreviation of MPD.

TABLE 2
Temporal and Geographical Distributions of Laurasian Dromaeosaurids

	Taxon	Locality	Formation	Age	Reference
1	*Achillobator giganitcus*	Dornogov, Mongolia	Bayanshiree Fm.	Cenomanian-Santonian	Perle, Norell, and Clark, 1999
2	*Adasaurus mongoliensis*	Bayankhongor, Mongolia	Nemegt Fm.	Senonian	Barsbold, 1983a
3	*Atrociraptor marshalli*	Alberta, Canada	Horseshoe Canyon Fm.	Late Campanian	Currie and Varricchio, 2004
4	*Bambiraptor feinbergorum*	Montana	Two Medicine Fm.	Campanian	Burnham et al., 2000
5	*Deinonychus antirrhopus*	Montana and Wyoming	Cloverly Fm.	l. Aptian or e. Albian	Ostrom, 1969a
6	*Dromaeosaurus albertensis*	Alberta, Canada	Dinosaur Park Fm.	Campanian	Matthews and Brown, 1922
7	*Hesperonychus elizabethae*	Alberta, Canada	Dinosaur Park Fm.	Campanian	Longrich and Currie, 2009
8	*Mahakala omnogovae*	Omnogov, Mongolia	Djadokhta Fm.	Campanian	Turner et al., 2007b
9	*Microraptor zhaoianus*	Liaoning, China	Yixian and Jiufotang Fms.	Aptian	Xu et al., 2000
10	*Graciliraptor lujiatunensis*	Liaoning, China	Yixian Fm.	Aptian	Xu and Wang, 2004
11	*Saurornitholestes langstoni*	Alberta, Canada	Dinosaur Park Fm.	Campanian	Sues, 1978
12	*Shanag ashile*	Omnogov, Mongolia	Oosh Fm.	Berriasian-Barremian	Turner et al., 2007a
13	*Sinornithosaurus millenii*	Liaoning, China	Yixian Fm.	Barremian/Aptian	Xu et al., 1999
14	*Tianyuraptor ostromi*	Liaoning, China	Yixian Fm.	Barremian/Aptian	Zheng et al., 2010
15	*Tsaagan mangas*	Omnogov, Mongolia	Djadokhta Fm.	Campanian	Norell et al., 2006
16	*Velociraptor mongoliensis*	Omnogov, Mongolia	Djadokhta Fm.	Campanian	Osborn, 1924b
17	*Velociraptor osmolskae*	Inner Mongolia, China	Bayan Mandahu Fm.	Campanian	Godefroit et al., 2008
18	*Utahraptor ostrommaysorum*	Utah	Cedar Mountain Fm.	Barremian	Kirkland et al., 1993
19	*Pyroraptor olympius*	La Boucharde, France	Begudian SS	Campanian-Maastrichtian	Allain and Taquet, 2000
20	*Balaur bondoc*	Alba County, Romania	Sebeş Fm.	Maastrichtian	Csiki et al., 2010

Therefore, these specimens are older (Cenomanian) than *Adasaurus*, which is known from the Maastrichtian age Nemegt Formation that overlies the Djadokhta Formation. This new taxon is reported to be distinguishable from all other dromaeosaurids in having two shallow subalveolar grooves on the labial surface of the dentary, a convex posterodorsal edge of ilium with a posteriorly curved distal end, and a transversely wide distal end on phalanx II-1 (Kubota and Barsbold, 2007). We have not been able to examine the postcranial remains of IGM 100/23, but the cranial remains indicate that the two shallow subalveolar grooves are not unique to this taxon. The paired rows of subalveolar nutrient foramina are prominent in other dromaeosaurid taxa like *Velociraptor mongoliensis* (AMNH FARB 6515) and *Dromaeosaurus albertensis* (AMNH FARB 5356). Since we have not seen the postcranial material we cannot comment on its similarity or dissimilarity with *Adasaurus mongoliensis*. Kubota and Barsbold (2007) recover IGM 100/23 + IGM 100/22 in a Dromaeosaurinae clade with *Dromaeosaurus* and *Achillobator*.

The skull of *Adasaurus mongoliensis* (IGM 100/20) is incomplete anterior to the preorbital bar (fig. 10). The right side is well preserved, whereas the left side is largely

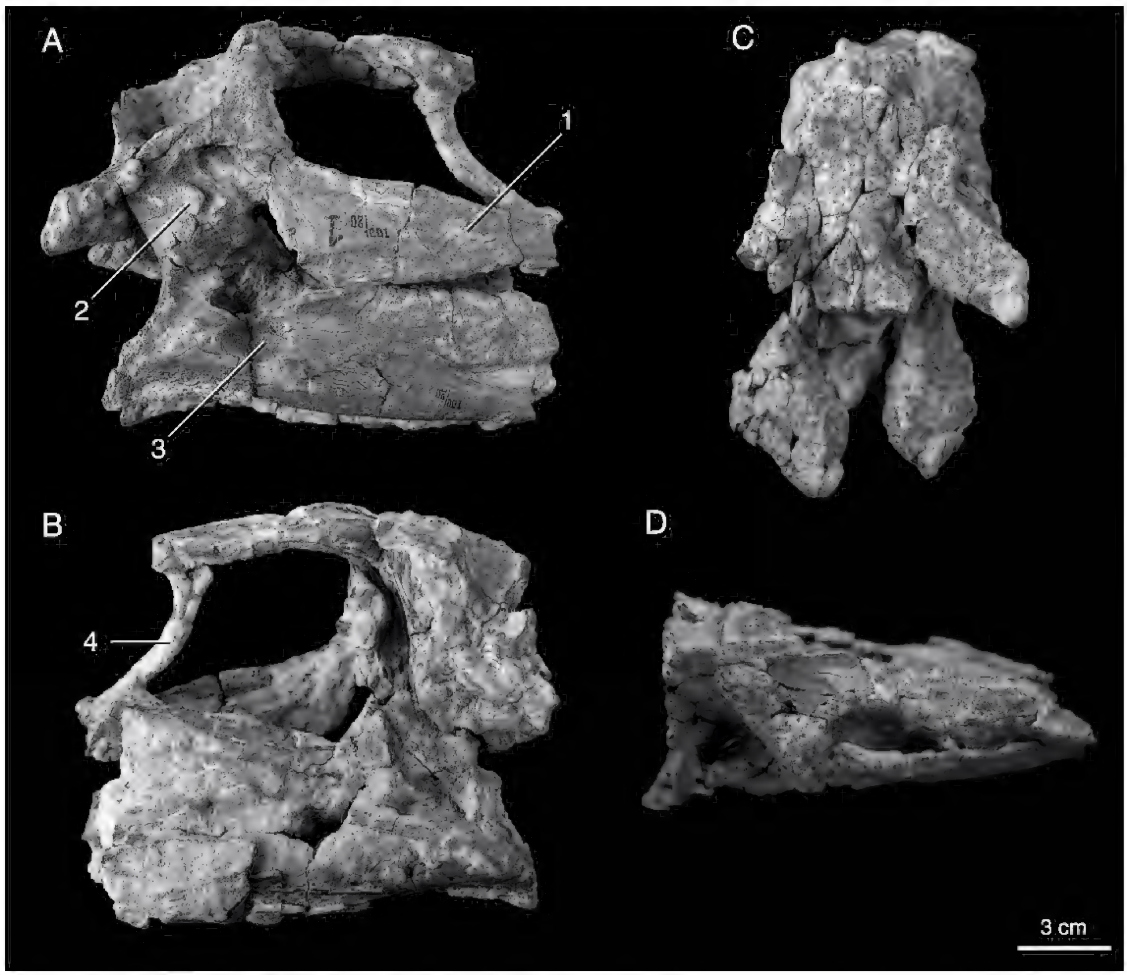


Fig. 10. Skull of *Adasaurus mongoliensis* (IGM 100/20). **A,** right lateral view; **B,** left lateral view; **C,** posterior view; **D,** dorsal view. 1, expanded maxillary process of jugal (char. 238.1); 2, dorsally displaced anterior process of quadrate; 3, large surangular foramen (char. 74.1); 4, anteriorly inclined lacrimal.

incomplete and insufficiently prepared and conserved. Across many parts of the skull, a thin layer of matrix remains on the bone partially obscuring the underlying morphology. On the right side it is apparent that the suborbital portion of the jugal is dorsoventrally expanded. The quadratojugal and the descending quadratojugal process of the squamosal are not preserved. The quadrate is large and vertically oriented. As in other dromaeosaurids, the lateral edge of the quadrate shaft is not straight but instead bears a large triangular process. Unlike other dromaeosaurids, the triangular process in *Adasaurus mongoliensis* is not centered on the quadrate shaft but is instead apomorphically shifted dorsally (fig. 10A). Unfortunately, the braincase is not visible. It is hoped that this important area of the skull will be CT scanned at some point in the near future. The right ectopterygoid is preserved, but the dorsal surface is compressed against the palate, so presence of a pneumatic recess cannot be ascertained. The lacrimal has an inverted L-shape as in other dromaeosaurids. The descending process of the lacrimal curves anteriorly to a large degree—a feature unique to *Adasaurus mongoliensis* and *Austroraptor cabazai*. Kubota and Barsbold (2006) suggest that there is a midline ridge on the dorsal surface of the frontal. Our examination of the holotype was unable to confirm this

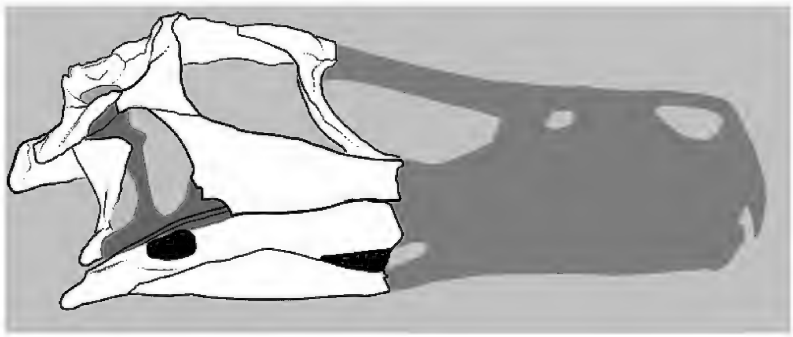


Fig. 11. Interpretive line drawing of the skull of *Adasaurus mongoliensis*.

observation, in part because much of the posterior portion of the frontal is incompletely prepared and is still obscured by a the thin layer of matrix. The completely exposed bone of the frontal lacks a ridge.

As discussed above, the ilium of IGM 100/20 is not pathological, and the often-reproduced illustration of Barsbold (1983a) is inaccurate in a number of ways that are clarified here. The dorsal edge of the ilium is straight and the pubic peduncle is wider and extends farther ventrally than the ischial peduncle (fig. 12). A large supratrochanteric process is absent. The anterior edge of the anterior blade of the ilium has a prominent anteriorly directed, dorsally displaced process similar to that seen in *Saurornitholestes langstoni*. Coupled with the large ventrally directed flange over the cuppedicus fossa, the anterior edge of the ilium has a "notched" appearance unlike the boxy, or square, margin seen in *Velociraptor mongoliensis* (IGM 100/25). The pes of IGM 100/21 is complete and well preserved. The ungual of digit II, which is apomorphically enlarged and trenchant in other deinonychosaurs, is small in *Adasaurus mongoliensis* (fig. 13). The proximal ends of the metatarsals on this pes are partially fused, suggesting that this individual was mature.

Recent phylogenetic analyses typically place *Adasaurus mongoliensis* in a large polytomy including all other dromaeosaurid taxa except *Sinornithosaurus millenii* and *Microraptor zhaoianus*, which are successive outgroups to the unresolved clade (Hwang et al., 2002; Makovicky et al., 2003; Xu and Norell, 2004). Senter et al. (2004) recovers *Adasaurus mongoliensis* as the sister group to a clade containing *Dromaeosaurus*, *Utahraptor*, *Achillobator*, *Deinonychus*, and *Saurornitholestes*. Novas and Pol (2005), Makovicky et al. (2005), and Turner et al. (2007a, 2007b) recover this taxon in an unresolved clade with *Achillobator*, *Dromaeosaurus*, and *Utahraptor*. Kubota and Barsbold (2006, 2007) have suggested a close relationship between *Velociraptor mongoliensis* and *Adasaurus*. Reexamination of the holotype material for the present study resulted in 102 changes to the taxon's scoring for existing characters plus numerous additional observations (table 3). This added information is critical for testing whether *Adasaurus* is in fact a dromaeosaurine, a velociraptorine, or a stem taxon.

Graciliraptor lujiatunensis Xu and Wang, 2004

Holotype: IVPP V13474 (fig. 14)

Distribution: Aptian, lowest member of Yixian Formation, Lujiatun, Beipiao City, western Liaoning, China.

Original Diagnosis: Following Xu and Wang (2004: 113–114), "a laminal structure connecting the postzygapophyses of middle caudals; extremely long and slender middle caudals; ungual of manual digit I much smaller than that of manual digit II; proximal end of metacarpal III strongly expanded; extremely slender tibiotarsus; proximal tibiotarsus shaft rectangular in cross section; astragular medial condyle significantly expanded posteriorly; metatarsal II distally much wider than the other metatarsals; and long slender pedal phalanx III-1."

Revised Diagnosis: A small dromaeosaurid diagnosed by the following combination

Fig. 12. Right ilium, ischium, and pubis of *Adasaurus mongoliensis* (IGM 100/20). Arrow indicates the notched anterior margin characteristic of *Adasaurus*.

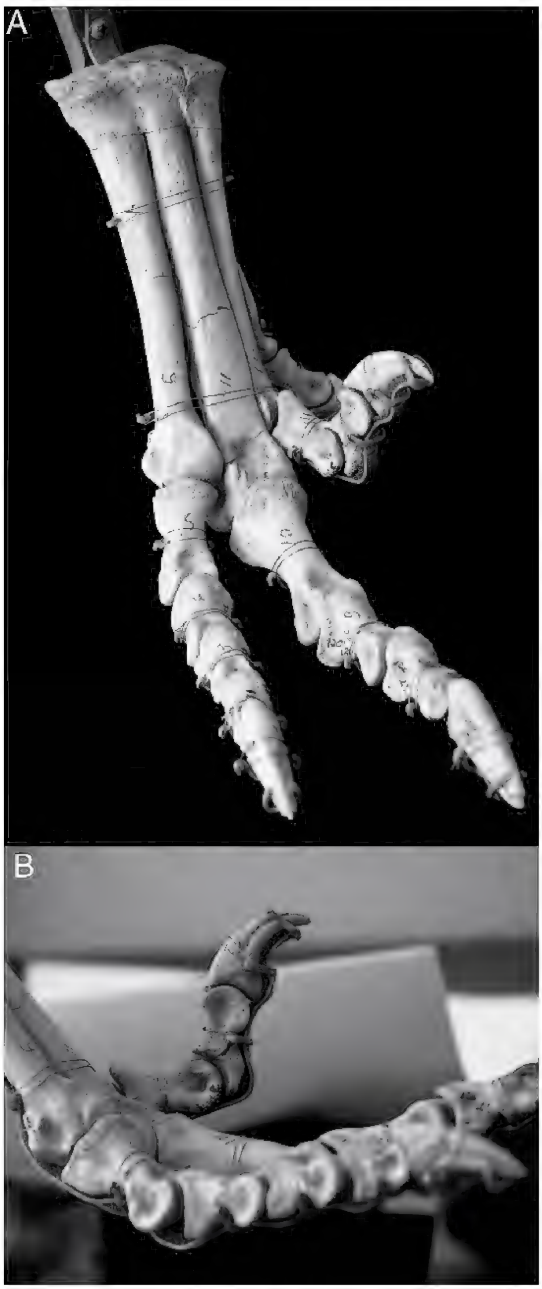


Fig. 13. Right pes of *Adasaurus mongoliensis* (IGM 100/20). **A,** anterolateral view; **B,** detail of digit II. The "reduced" ungual phalanx on digit II is autapomorphic for *Adasaurus*.

of characters and autapomorphies: extremely long midtail caudals (shared with *Microraptor zhaoianus*); extremely slender tibiotarsus; medial condyle of tibiotarsus significantly expanded posteriorly*; metatarsal II distally much wider than other metatarsals.

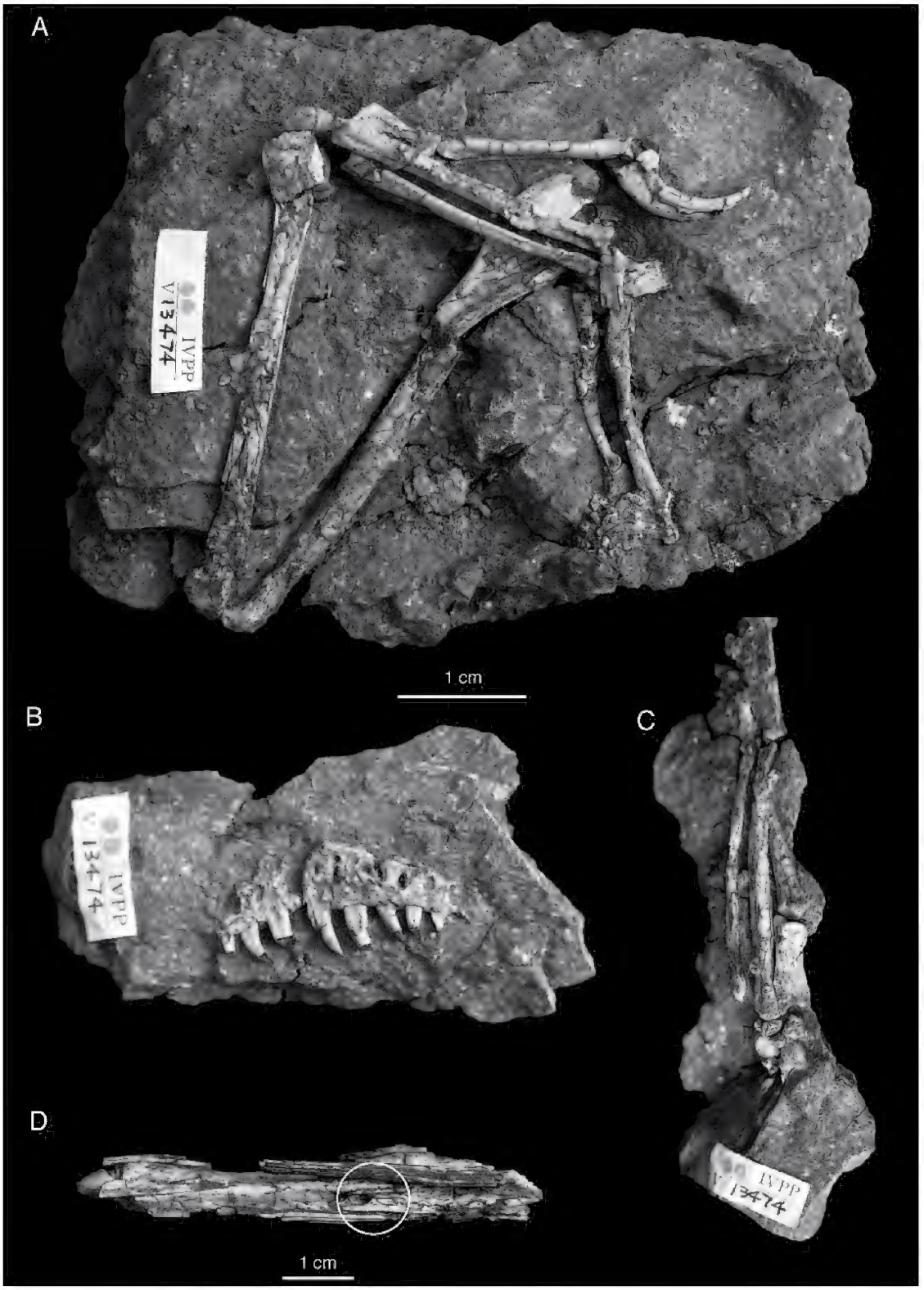
DISCUSSION: Based on a partial skeleton including forelimb and hindlimb material and a partial maxilla, *Graciliraptor lujiatunensis* is the least well-known Yixian dromaeosaurid (Xu and Wang, 2004). Originally considered the oldest known dromaeosaurid based on earlier stratigraphic work in the Lujiatun beds (Zhou et al., 2003), these beds are now considered contemporaneous with the Jianshangou beds (He et al., 2006) and therefore approximately Aptian in age. Scorings in our matrix are based on examination of the holotype specimen. *Graciliraptor* has been included in only two phylogenetic analyses (Xu and Wang, 2004; Turner et al., 2007b) and in both of these the taxon was recovered in a clade with *Sinornithosaurus* and *Microraptor*.

Of the nine original characters proposed to diagnose *Graciliraptor lujiatunensis* only four appear to stand up to scrutiny. Moreover, only one character appears to be autapomorphic for the taxon (medial condyle of tibiotarsus significantly expanded posteriorly) but this character is difficult to examine in other microraptorines, as most are preserved in two dimensions. Indeed, future discoveries of *Graciliraptor*-like specimens and continued work on *Microraptor* may show the two to be conspecific. Nonetheless, in our opinion, *Graciliraptor lujiatunensis* can be diagnosed by the unique combination of characters listed above until evidence to the contrary is discovered or published.

A few characters proposed as diagnostic by Xu and Wang (2004) prove to be problematic when considered in the broader context of dromaeosaurid variation. The laminar structure connecting the postzygapophyses of middle caudals noted by Xu and Wang (2004) is widespread among dromaeosaurids (fig. 14D). This laminar structure is a posterior extension of the neural arch that supports the base of the neural spine in successive caudal vertebrae. The structure is present in the dromaeosaurids *Rahonavis ostromi* (UA 8656), *Buitreraptor gonzalezorum* (MPCA 245), *Adasaurus mongoliensis* (IGM 100/20), *Velociraptor mongoliensis* (IGM 100/986), and *Deinonychus antirrhopus* (Ostrom, 1969a), as well as in more basal coelurosaurs such as *Ornitholestes hermanni* (AMNH FARB 619).

TABLE 3
Revised Character Scorings for *Adasaurus mongoliensis*.

Character Number	Previous Scoring (Turner et al., 2007b)	Revised Scoring (this paper)
2	?	0
3	?	1
4	?	1
5	?	0
11	?	0
16	?	2
31	?	0
37	?	0
42	?	1
43	?	1
45	?	1
47	?	0
49	?	1
50	?	0
51	?	0
52	?	0
53	?	1
56	?	0
57	?	0
58	?	1
61	?	0
67	?	0
72	?	0
74	?	1
78	?	0
80	0	?
85	0	?
92	?	0
93	?	1
94	?	1
95	?	0
96	?	1
98	?	1
99	?	1
101	?	0
102	?	1
103	?	1
104	?	1
106	?	1
107	?	0
109	?	1
110	?	1
111	?	1
112	?	0/1
113	?	1
114	?	0
115	?	0
118	?	0
119	?	1
120	?	1
122	?	1
124	?	1
131	?	1
133	?	1
134	?	1
135	?	1
136	?	1
137	?	1
138	?	1
155	?	0
161	?	0
176	?	1
179	?	1
181	?	0
184	?	1
185	?	1
186	?	1
187	?	0
188	?	0
189	?	0
190	?	0
191	?	0
192	?	0
194	?	0
195	?	0
196	?	0
198	?	0
199	?	1
200	?	0
201	?	1
202	?	0
205	?	0
206	?	0
207	?	1
211	?	0
212	?	0
216	?	0
217	?	1
218	?	0
219	?	0
220	0	?
221	?	0
222	?	?
223	?	0
224	?	?
225	?	0
226	?	0
227	?	0
235	?	0
238	?	1
245	?	1
246	?	1


A
IVPP
V13474
1 cm
B
IVPP
V13474
C
IVPP
V13474
D
1 cm

The extremely long middle caudals cited by the authors as unique to *Graciliraptor* are in fact shared with *Microraptor* (IVPP V13352) and are potentially a synapomorphy for the pair. We are unable to confirm two other observations regarding *Graciliraptor*. First, it is unclear whether the ungual of manual digit I is much smaller than that of manual digit II. The digit I ungual is the best preserved; the digit II ungual is poorly preserved and was severely crushed, rendering it difficult to gauge how large it is proximally (fig. 14A). Additionally, we could not confirm the observation of a strongly expanded metacarpal III. It looks slender and no more dorsoventrally expanded than metacarpal II.

Both an extremely slender tibiotarsus and a long slender pedal phalanx III-1 was used to diagnose *Graciliraptor lujiatunensis*. Both features are also present in *Microraptor*, and it seems reasonable that the slenderness is probably allometric. Lastly, the proximal portion of the tibiotarsus shaft is rectangular in cross section. We find this a weak characteristic. In *Buitreraptor gonzalezorum* (MPCA 245), *Rahonavis ostromi* (UA 8656), and *Velociraptor mongoliensis* (IGM 100/986) the tibia is rectangular in the same spot.

Linheraptor exquisitus Xu et al., 2010

Holotype: IVPP V16923.

Distribution: Campanian, Late Cretaceous, Bayan Mandahu Formation (Wulansuhai Formation), Inner Mongolia, China.

Original Diagnosis: Following Xu et al. (2010), a "dromaeosaurid that can be distinguished from other known dromaeosaurid taxa by the presence of the following autapomorphies: greatly enlarged maxillary fenestra sub-equal in size to external naris; several large foramina on lateral surface of jugal. Differs from other known dromaeosaurids except *Tsaagan* in the following features: large and anteriorly located maxillary fenestra; lacrimal lacking lateral flange over descending process and with relatively broad medial lamina; sharp angle between anterior and ascending processes of quadratojugal; contact between jugal and squamosal that excludes postorbital from infratemporal fenestra. Differs from *Tsaagan* in the following features: absence of osseous inner wall partly blocking antorbital fenestra; sharply rimmed ventral margin of antorbital fossa; considerably smaller angle between frontal and jugal processes of postorbital; anteroventrally curved postorbital process of squamosal; considerably shorter quadratojugal process of squamosal; dorsoventrally shorter lateral flange of quadrate; less curved and less posteriorly inclined quadrate shaft; paroccipital process more laterally oriented; angular more extended posteriorly toward glenoid fossa; considerably deeper posterior end of mandible such that glenoid fossa is approximately level with tooth row; pneumatic foramen present on axis vertebra."

Revised Diagnosis: Not applicable. This taxon is here considered a junior synonym of *Tsaagan mangas*. (see fig. 15).

Discussion: Xu et al. (2010) provided eleven putative autapomorphies diagnosing *Linheraptor exquisitus*. This taxon is strikingly similar to the contemporaneous *Tsaagan mangas* from the Ukhaa Tolgod locality, Djadokhta Formation of Mongolia. The autapomorphies for *Linheraptor* were provided to distinguish it from *Tsaagan*. A review of these features reveals that they fail to differentiate these two taxa.

Xu et al. (2010) indicate that an absence of an internal osseous medial wall within the antorbital fenestra differs from the condition in *Tsaagan* in which such a medial wall is present posterior to the anterior margin of the internal antorbital fenestra. However, this trait cannot be used to diagnose *Linheraptor*. The holotype skull (IVPP V16923) was not prepared far enough (or CT scanned) to confirm the presence or absence on the

←

Fig. 14. Select holotype material of *Graciliraptor lujiatunensis* (IVPP V13474). **A,** right forelimb; **B,** left partial maxilla; **C,** right manus; **D,** two distal caudal vertebrae. In **D,** the circle highlights the lamina that extends between the postzygapophyses.

Fig. 15. Comparison of *Linheraptor exquisitus* (IVPP V16923) with *Tsaagan mangas* (IGM 100/1015). **A,** skull of *Tsaagan mangas* in right lateral view; **B,** skull of *Linheraptor exquisitus* in right lateral view; **C,** skull of *Tsaagan mangas* in left lateral view (reversed for comparative purposes).

internal osseous medial wall as in *Tsaagan* and *Velociraptor*.

Xu et al. (2010) additionally suggest that the ventral margin of the antorbital fossa is more sharply rimmed and demarcated in *Linheraptor* than in *Tsaagan*. Examination of the skulls of the IVPP V16923 and IGM 100/1015 clearly shows that little to no difference exists in the degree to which the ventral rim of the antorbital fossa is demarcated. The antorbital fenestra and fossa remain nearly identical between these two specimens.

According to Xu et al. (2010), in *Linheraptor* the angle between the frontal and jugal processes of the postorbital is smaller (roughly 90°) than the same angle in *Tsaagan* (roughly 135°). By our calculations, the angle between these two processes is closer to 95° in *Linheraptor* and 100° in *Tsaagan*. However, it is not so much that the angle between the frontal and jugal processes are greater in *Tsaagan*, but rather that the anterior margin of the postorbital is less concave in lateral aspect in *Tsaagan* relative to *Linheraptor*. Nevertheless, this is a very subtle difference and well within the range of variation one sees within specimens of *Velociraptor* (Norell et al., 2006: fig. 6). Therefore, this feature should not be considered diagnostic for *Linheraptor exquisitus*.

The fourth feature used to distinguish *Linheraptor* from *Tsaagan* is the curvature of the postorbital process of the squamosal. In the initial description of *Linheraptor* it was noted that the postorbital process of the squamosal in *Linheraptor* curves distinctly ventrally whereas the same process in *Tsaagan* is straight. We see very little curvature in the postorbital process of the squamosal in *Linheraptor*. Only the distalmost portion of the process shows any curvature and the "distinct" nature of this curvature may be accentuated by a fracture running through the process in IVPP V16923. The postorbital process of the squamosal in *Tsaagan* is not completely straight. It too has some curvature on its path along the ventral aspect of the postorbital (Norell et al., 2006: fig. 9). The apparent "straightness" of the process is perhaps accentuated on the left side of the skull due to slight damage at the confluence of the postorbital and quadratojugal processes. Thus, as with the previous putative autapomorphies, we do not consider the squamosal morphology distinct between these two taxa.

Two additional putative autapomorphies for *Linheraptor* pertain to the size of the quadratojugal process of the squamosal and the dorsoventral height of the lateral flange of the quadrate. Xu et al. (2010) considered the quadratojugal process of the squamosal in *Linheraptor* to be shorter than that in *Tsaagan*. We were not able to replicate this observation. When the two skulls are scaled to the same size the quadratojugal process of the squamosal is identical between the two specimens (IVPP V16923 and IGM 100/1015). In the unscaled skulls, the two processes both measure roughly 14 mm in length. With only about 20 mm difference in total skull length between the two animals, we see little difference with respect to this trait especially because some of this length may be ascribable to deformation. Similarly, the lateral flange of the quadrate was said to be dorsoventrally shorter in *Linheraptor* than in *Tsaagan*; however, when the skulls are again scaled to the same size there is no difference in the dorsoventral height of the lateral flange of the quadrate (8 mm in height at its anterior edge in both *Linheraptor* and a scaled *Tsaagan*).

Xu et al. (2010) suggest that the quadrate shaft is less curved and less posteriorly inclined in *Linheraptor* relative to *Tsaagan*. This apparently less curved and less posteriorly inclined quadrate is indeed present when you compare the holotype skull of *Tsaagan* with that of *Linheraptor*. However, the difference is not real, but instead it is a preservational artifact of the more severe mediolateral compression in the *Tsaagan* holotype (see Norell et al., 2006: figs. 3A, F, 14). When one corrects for the compression or views the quadrate of *Tsaagan* in isolation (e.g., Norell et al., 2006: fig. 10C) the inclination of the quadrate is nearly identical to that of *Linheraptor*.

One additional feature used to distinguish *Linheraptor* from *Tsaagan* is similarly affected by the mediolateral compression of the *Tsaagan* holotype skull. Xu et al. (2010) suggest that the paroccipital processes are more laterally oriented in *Linheraptor* than in *Tsaagan*. The paroccipital processes are in

fact laterally oriented in *Tsaagan* (Norell et al., 2006: figs. 3, 13); however, as noted by Norell et al. (2006: 19), the posterior end of the skull of *Tsaagan* was compressed mediolaterally during preservation. We conclude that without this compression no difference would exist as a basis for distinction between *Tsaagan* and *Linheraptor*.

Two features pertaining to the posterior end of the mandible were used to diagnosis *Linheraptor*. One was that the angular extends more posteriorly in *Linheraptor* than in *Tsaagan*, and the second was that the posterior end of the mandible was overall deeper (dorsoventrally taller) in *Linheraptor* than in *Tsaagan* (Xu et al., 2010). In *Linheraptor*, the angular extends to the posterior margin of the posterior surangular foramen, whereas it extends to the anterior margin of the posterior surangular foramen in *Tsaagan*. This is roughly a 6 mm difference in the posterior extent of the angular (a similar difference is observed by measuring from the posterior end of the angular to the posterior edge of the glenoid fossa). We do not view this subtle degree of variation as sufficient to be an autapomorphy for a new taxon, especially in skulls that have both suffered some degree of deformation. With regard to the dorsoventral height of the posterior end of the mandible, we were unable to confirm the observation that this portion of the mandible is dorsoventrally taller in *Linheraptor*. Once again, when the two skulls are scaled to the same size, there is effectively no difference in dorsoventral height when measured from the apex of the coronoid process to the base of the mandible (~30 mm in *Linheraptor* and ~32 mm in *Tsaagan* when scaled to the skull length of *Linheraptor*).

The final autapomorphy used to distinguish *Linheraptor* from *Tsaagan* is the presence of a pneumatic foramen on the axis of *Linheraptor* that is not present on the axis of *Tsaagan*. This appears to be the only clear difference between *Linheraptor* and *Tsaagan*. However, vertebral pneumaticity can be variable within dromaeosaurids—notably *Velociraptor mongoliensis* shows variation in the axis pneumaticity (IGM 100/24 lacks a foramen, but IGM 100/976 has one) and dorsal vertebrae pneumaticity (IGM 100/24 dorsals have foramina, but IGM 100/986 lacks them). We do not think this is sufficient grounds to serve as the sole justification for erecting a new taxon.

Linheraptor exquisitus (known only from IVPP V16923) and *Tsaagan mangas* (known only from IGM 100/1015) are effectively identical in the areas where the two specimens overlap. As illustrated in the discussion above, the 11 putative autapomorphies for *Linheraptor* fail to distinguish IVPP V16923 from IGM 100/1015. Moreover, given the presence of three *Tsaagan mangas* autapomorphies in IVPP V16923 (paroccipital process that is pendulous and not twisted distally; maxillary fenestra that is large and located at the anterior edge of the antorbital fossa; jugal that meets the squamosal to exclude the postorbital from the margin of the infratemporal fenestra), we conclude here that *Linheraptor exquisitus* is not a valid taxon but is instead a junior synonym of *Tsaagan mangas*. This conclusion is interesting because it adds additional support to the documented faunal similarity between the Campanian Djadokhta Formation of southern Mongolia and the Campanian Bayan Mandahu Formation of northern Inner Mongolia.

Mahakala omnogovae Turner et al., 2007

Holotype: IGM 100/1033 (figs. 16–18).

Distribution: Campanian, Late Cretaceous, Tögrögiin Member of the Djadokhta Formation, Tögrögiin Shiree, Ömnögov Mongolia.

Original Diagnosis: Following Turner et al. (2007b: 1378), a "small paravian diagnosed by the following combination of characters: a strongly compressed and anteroposteriorly broad ulna tapering posteriorly to a narrow edge*; elongate lateral crest on the posterodistal femur*; anterior caudal vertebrae with subhorizontal, laterally directed prezygapophyses*; a prominent supratrochanteric process; and the absence of a cuppedicus fossa."

Revised Diagnosis: A small dromaeosaurid diagnosed by the following combination of characters and autapomorphies: ledge-like depression ventrally located at confluence of metotic strut and posterior tympanic recess

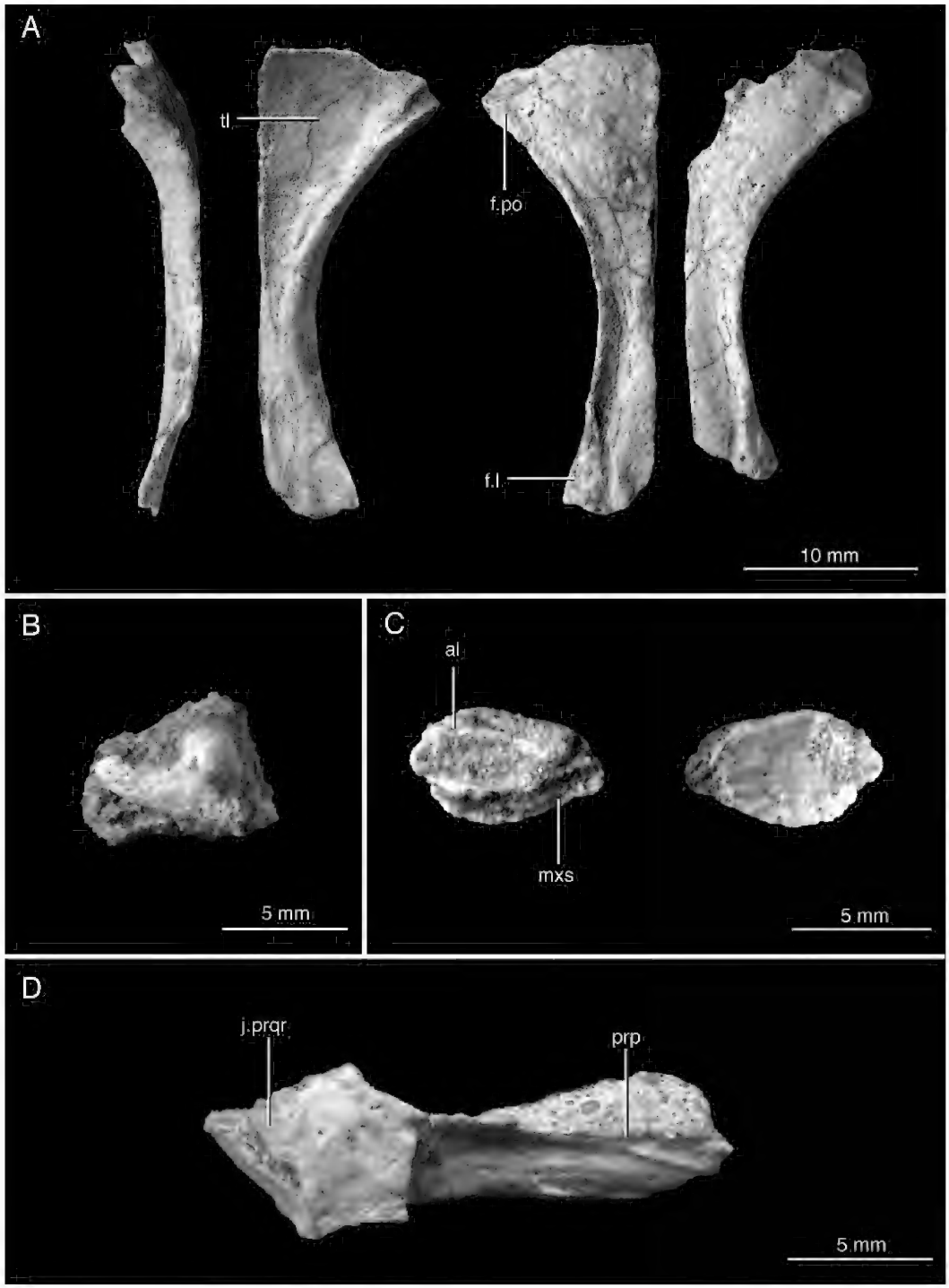


Fig. 16. Select skull material of *Mahakala omnogovae* (IGM 100/1033). **A,** (left to right) right frontal in lateral view, internal view, dorsal view, and left frontal in dorsal view; **B,** possible right ectopterygoid; **C,** left maxilla in medial (left) and lateral (right) views; **D,** partial right pterygoid in dorsal view.

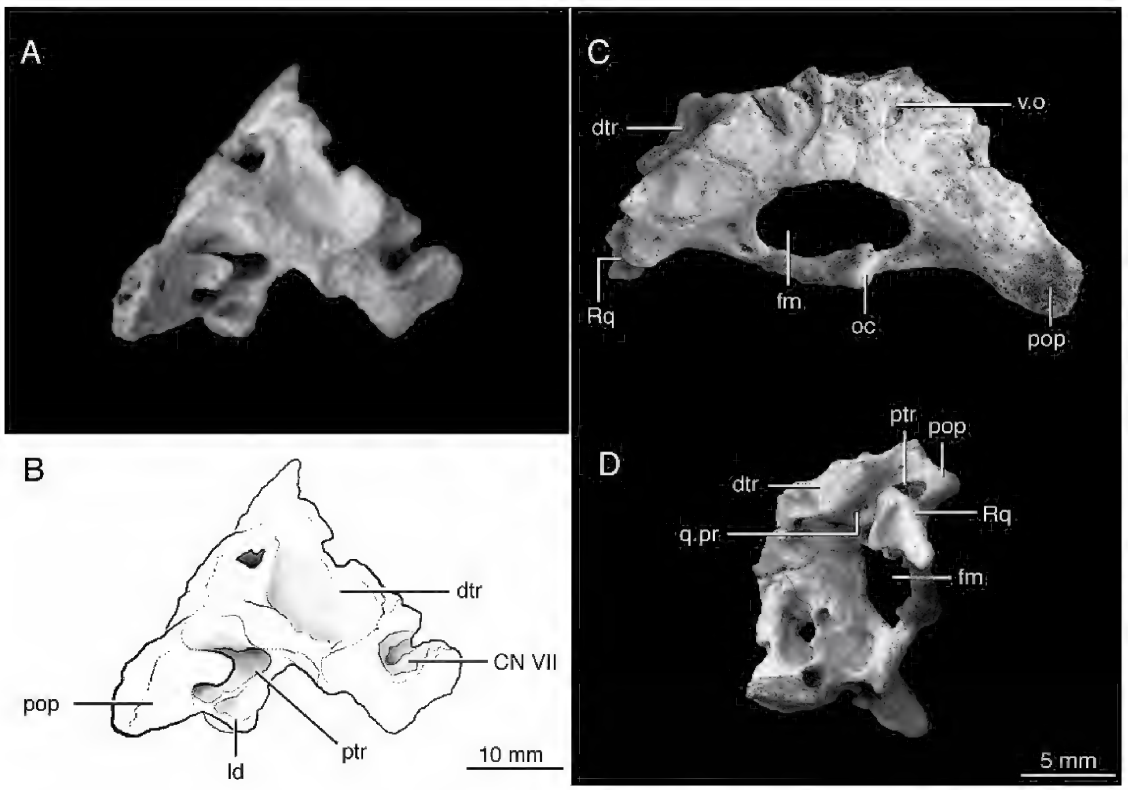


Fig. 17. Holotype cranium of *Mahakala omnogovae* (IGM 100/1033). **A,** right lateral view; **B,** interpretive line drawing of right lateral view; **C,** posterior view; **D,** left ventrolateral view.

on anterior face of paroccipital process*, posteriorly tapering scapula; shortened forelimb (humerus ~50% femur length); strongly mediolaterally compressed and anteroposteriorly broad ulna tapering posteriorly to narrow edge*; elongate lateral crest on posterodistal end of femur*; anterior caudal vertebrae with subhorizontal, laterally directed prezygapophyses*; prominent supratrochanteric process; and absence of cuppedicus fossa.

DISCUSSION: Turner et al. (2007b) gave a preliminary description of this taxon, which was followed by a longer, more complete and well-illustrated description (Turner et al., 2011). In the accompanying phylogenetic analysis of Turner et al. (2007b), *Mahakala* was found to be the basalmost dromaeosaurid based on the absence of an accessory tympanic recess dorsal to the crista interfenestralis, the presence of an elongate paroccipital process with parallel dorsal and ventral edges that twist rostrolaterally distally, and the presence of a distinct ginglymus on the distal end of metatarsal II. *Mahakala* lacks the elongate prezygapophyses and chevrons present in more derived dromaeosaurids and also lacks the subarctometatarsalian pes seen in microraptorine dromaeosaurids. As this taxon was a focus of a contemporary study (Turner et al., 2011) it will not be discussed further here.

MICRORAPTOR GUI XU ET AL., 2003

HOLOTYPE: IVPP V13352 (fig. 19).

DISTRIBUTION: Aptian-Albian, Early Cretaceous, Jiufotang Formation, Xiasanjiazi, Chaoyang County, western Liaoning.

ORIGINAL DIAGNOSIS: Following Xu et al. (2003: 335), "distinguishable from *Microraptor zhaoianus* in having prominent biceps tuberosity on radius, much shorter manual digit I, strongly curved pubis, and bowed tibia."

REVISED DIAGNOSIS: Not applicable. This taxon is here considered a junior synonym of *Microraptor zhaoianus* (see fig. 20 and table 4).

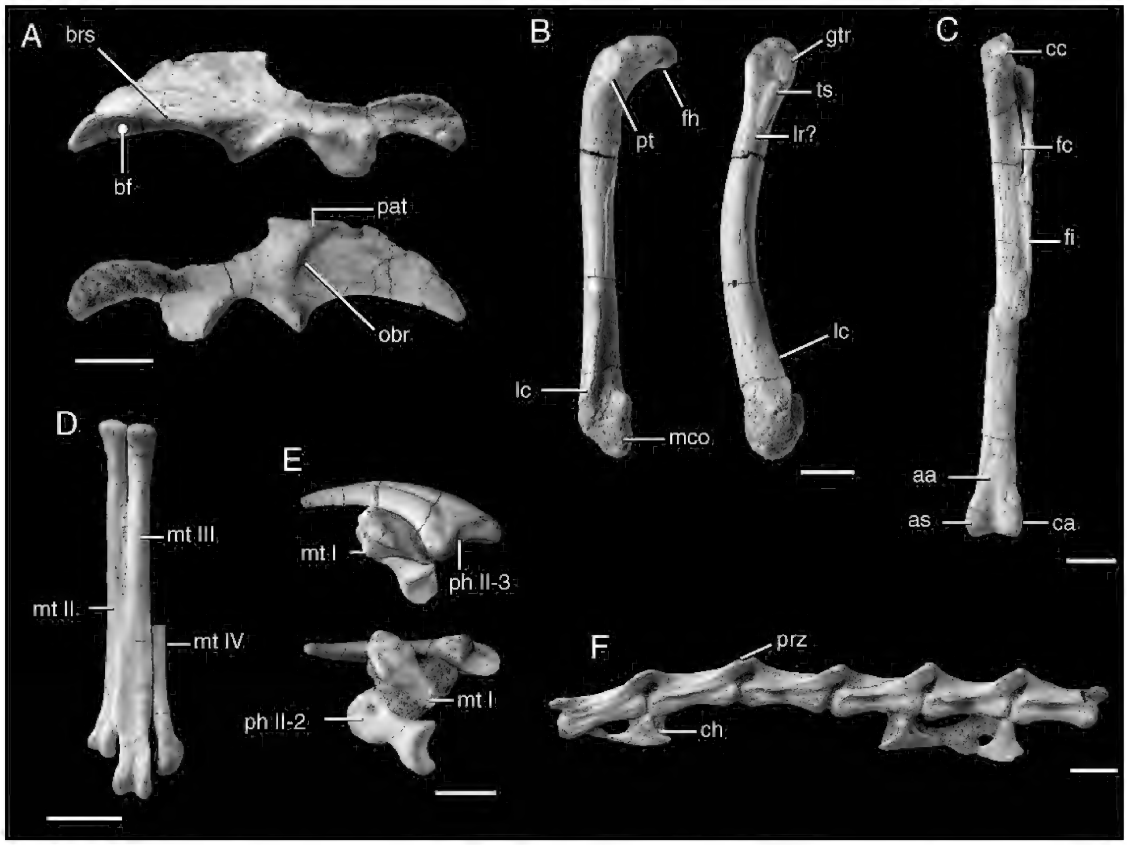


Fig. 18. Select postcranial remains of *Mahakala omnogovae* (IGM 100/1033). **A,** left ilium in medial (upper) and lateral (lower) views illustrating a large postacetabular tuber (char. 160.1); **B,** left femur in posterior (left) and lateral (right) views illustrating the presence of a posterior trochanter (char. 414.0/1); **C,** left tibia in anterior view; **D,** left metatarsus in anterior view; **E,** left pedal phalanges; **F,** caudal vertebrae 9 through 14 in right lateral view. See appendix 6 for abbreviations.

Discussion: This taxon was described on the basis of two nearly complete specimens (IVPP V13352, which is the holotype; and IVPP V13320) from the Lower Cretaceous Jehol Group, Jiufotang Formation of the Chaoyang Basin. It is interesting for its preservation of pennaceous, remexlike feathers on its hindlimbs. Fourteen large feathers are preserved on the metatarsus with the proximal ones shorter in length and possessing symmetrical vanes. The distal feathers are longer and possess asymmetrical vanes. Pennaceous feathers are also present on the tibia.

The prominent biceps tubercle present on the radius of IVPP V13352 is unknown in the referred *Microraptor gui* specimen (IVPP V13320). A large biceps tubercle is also present in an uncataloged IVPP specimen. This character is, however, variably present in *Microraptor zhaoianus* (IVPP V12330 and CAGS 20-8-001) and its presence is unknown in six of the other known *Microraptor* specimens (fig. 20). Given the variable presence of this character in *Microraptor zhaoianus*, its uncertain distribution among other *Microraptor* specimens, and possible ontogenetic variability of this characteristic we considered it undiagnostic for *Microraptor gui,* but a variable feature for *Microraptor* in general.

Manual digit I is not preserved in any of the referred *Microraptor zhaoianus* specimens (IVPP V12330, CAGS 20-8-001, CAGS 20-7-004), so the proportionally short manual digit I cannot be used to distinguish *Microraptor gui* from *Microraptor zhaoianus*. In

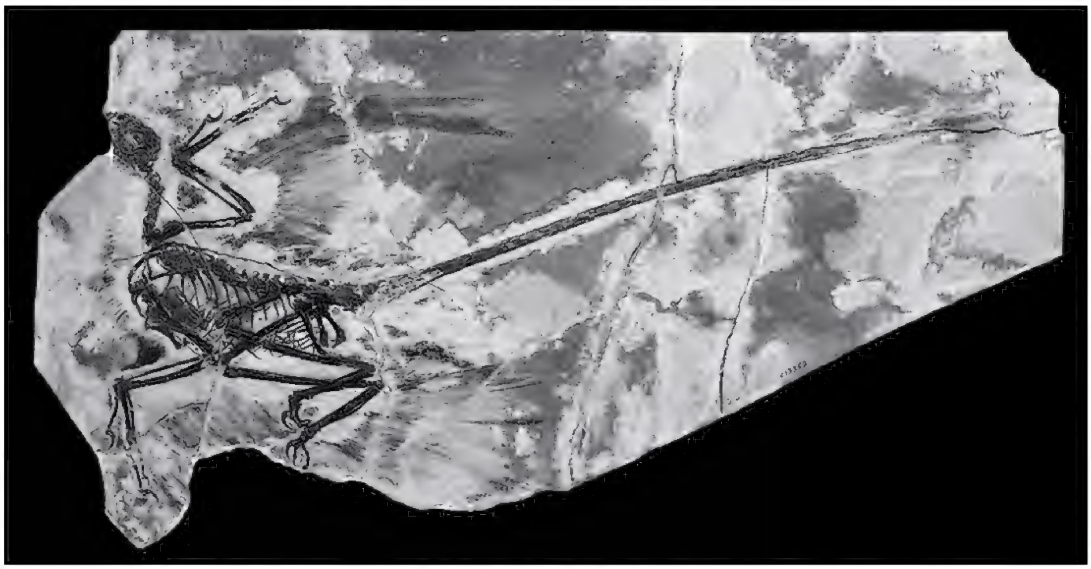


Fig. 19. Holotype of *Microraptor gui* (IVPP V13352).

fact, a proportionally short manual digit I is present in *Sinornithosaurus millenii* (IVPP V12811, NGMC 91), *Microraptor gui* (IVPP V13352, IVPP V13320), and two uncataloged IVPP *Microraptor* specimens to the exclusion of *Graciliraptor lujiatunensis* and other dromaeosaurids. In *Microraptor gui* the length of metacarpal I is 43% (IVPP V13352) or 47% (IVPP V13320) that of metacarpal II. In two uncataloged IVPP specimens of *Microraptor* metacarpal I is 44% and 48% respectively, whereas in, *Sinornithosaurus millenii* metacarpal I is 49% (NGMC 91) or 42% (IVPP V12811) that of metacarpal II.

As written, "a strongly curved pubis" is ambiguous and therefore problematic. This character refers to a strongly posteriorly curved pubis. Many *Microraptor* specimens are compressed dorsoventrally (BPM 1 3-13, CAGS 20-8-001, CAGS 20-7-004, IVPP V12330, IVPP V13320, IVPP V12727, IVPP V13476, IVPP V200211, and two uncataloged IVPP specimens) as is one specimen of *Sinornithosaurus* (NGMC 91). In specimens that are mediolaterally compressed, the pubis of *Microraptor* (IVPP V13352, uncat. 2) and *Sinornithosaurus* (IVPP V12811) are posteriorly curved, so that the posterior surface is concave. Thus, like a proportionally short manual digit I, a strongly posteriorly curved pubis is likely a *Microraptor* + *Sinornithosaurus* synapomorphy, although a lesser degree of posterior curvature is present in many dromaeosaurids (e.g., *Unenlagia*, *Velociraptor*, *Deinonychus*) and in some basal troodontids (e.g., *Sinovenator*, *Sinusonasus*, *Anchiornis*). The presence of some degree of posterior curvature of the pubis may prove to be more broadly characteristic of basal deinonychosaurs.

A bowed tibia is present in only one specimen of *Microraptor gui* (IVPP V13320); the holotype specimen (IVPP V13352) lacks a bowed tibia (fig. 20). The tibiae of *Microraptor zhaoianus* also display this variability—IVPP V12330 has a bowed tibia while CAGS 20-8-001 and CAGS 20-7-004 lack a bowed tibia. Five additional *Microraptor* specimens display an unbowed tibia (IVPP V13352, IVPP V12727, IVPP uncataloged 1, IVPP uncataloged 2, and IVPP uncataloged 3). Given the predominance of unbowed tibiae among *Microraptor* specimens and that in both cases where bowing is observed, the specimens are poorly preserved and are preserved in a splayed posture, we view this bowing as preservational and not diagnostic of a particular *Microraptor* taxon. Indeed, many of the specimens from the "Jehol localities" are severely plastically deformed

(for instance, see the *Sapeornis* specimen described by Yuan, 2008) and subtle differences in curvature and orientation are often difficult to interpret.

Of the originally proposed characters diagnosing *Microraptor gui* none remain to distinguish it from *Microraptor zhaoianus*. Therefore, we consider *Microraptor gui* a junior synonym of *Microraptor zhaoianus*. All specimens of *Microraptor zhaoianus* and *Microraptor* "*gui*" (when the relevant anatomy is preserved) possess a basal constriction of the teeth (except IVPP V13320), midcaudals that are three to four times the length of the dorsal vertebrae, an accessory crest distal to the lesser trochanter, and a strongly posteriorly curved pubis.

Microraptor zhaoianus Xu et al., 2000

Holotype: IVPP V12330 (fig. 21).

Distribution: Aptian-Albian, Early Cretaceous, Yixian and Jiufotang Formations, Xiasanjiazi, Chaoyang County, western Liaoning.

Original Diagnosis: Following Xu et al. (2000: 705), "distinguishable from all other dromaeosaurids in anterior serrations absent on all teeth; posterior teeth have a basal constriction; middle caudals are about three to four times as long as the anterior dorsals; accessory crest of femur at the base of the lesser trochanter; tail with less than 26 vertebrae; and it has a strongly recurved and slender pedal ungual with prominent flexor tubercle." This diagnosis was based on IVPP V12330.

Revised Diagnosis: A small dromaeosaurid diagnosed by the following combination of characters and autapomorphies: anterior serrations absent on all teeth; posterior teeth with basal constriction; middle caudal vertebrae about three to four times as long as anterior dorsals*; accessory crest on femur at base of lesser trochanter; tail with less than 26 vertebrae; extremely long and bowed metatarsal V*; and strongly recurved and slender pedal ungual with prominent flexor tubercle.

Discussion: *Microraptor zhaoianus* is one of the smallest nonavian dinosaurs known. The holotype specimen (IVPP V 12330) has a femur length of only 53 mm and an estimated body length of 470 mm (although in the initial publication a typo suggested that the animal was only 47 mm long). Subsequently, larger individuals of *Microraptor* have been found, some with femoral lengths nearly twice that of the holotype (IVPP V13320) and a thorough description was given by Hwang et al. (2002). As discussed above, we regard all specimens of *Microraptor* as belonging to a single species *Microraptor zhaoianus*. The characters originally used to diagnosis *M. zhaoianus* are present in specimens of *Microraptor* "*gui,*" and as outlined above the characters used to distinguish *M.* "*gui*" from *M. zhaoianus* are not valid or are more widespread.

Shanag ashile Turner et al., 2007

Holotype: IGM 100/1119 (fig. 22).

Distribution: Berriasian–Barremian; Öösh Formation, Öösh locality, Ovorkhangai Aimag, Mongolia.

Diagnosis: Following Turner et al. (2007a: 4), a "small dromaeosaurid diagnosed by the following combination of characters: triangular, anteriorly tapering maxilla; lateral lamina of nasal process of maxilla reduced to small triangular exposure; absence of a promaxillary fenestra*; presence of interalveolar pneumatic cavities*; incipient dentary groove on posterolateral surface of dentary."

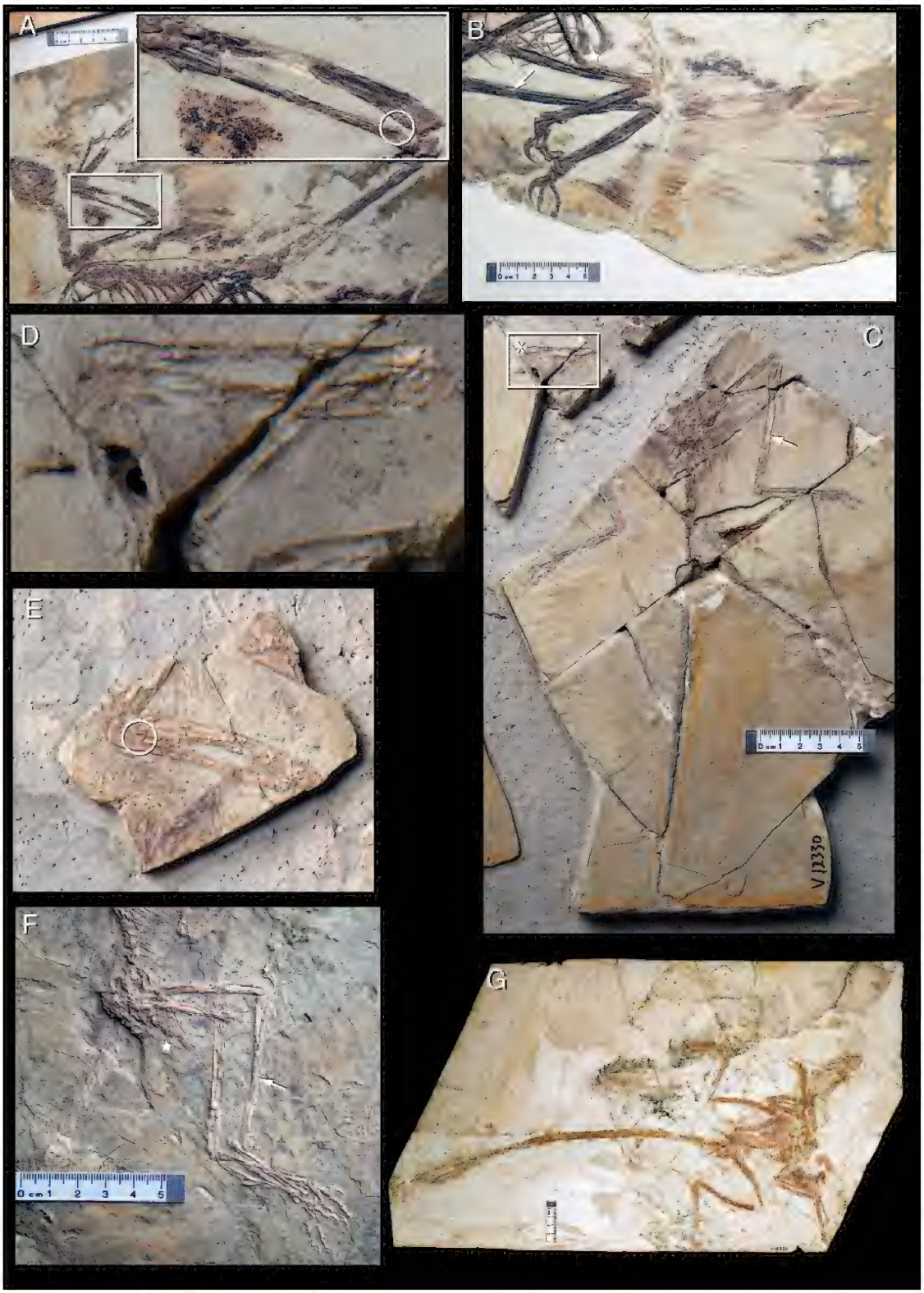
Discussion: This taxon is known from a single fragmentary specimen with only cranial material preserved. The material consists of a right maxilla, dentary and splenial. Postcranial material from a small arctometatarsalian theropod recently described from Öösh by (Prieto Marquez et al., 2011) may be referable to this taxon, but there is no overlap between the two specimens aside from a small fragment of maxilla. Character scoring in our analysis is based entirely on the holotype material from Öösh and originally identified by Turner et al. (2007a).

Sinornithosaurus haoiana Liu et al., 2004

Holotype: D 2140.

Distribution: Early Cretaceous, Yixian Formation, Toutai, western Liaoning, China.

Original Diagnosis: Following Liu et al. (2004: 783), "distinguished from *S. millenii* in that: (1) the main body of the premaxilla is higher, its length being slightly longer than its height; (2) the anterior margin of the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premaxilla is vertical; (3) the maxillary process of the premaxilla is very long; (4) the maxilla is separated from the external naris; (5) maxillary fenestra is circular and relatively small; (6) the ascending process of the quadratojugal is remarkably longer than the jugal process; (7) the ratio of the dentary length/height is distinctly small; and (8) the pubic peduncle of ilium is longitudinally narrower than acetabulum."

REVISED DIAGNOSIS: Not applicable. This taxon is here considered a junior synonym of *Sinornithosaurus millenii*.

DISCUSSION: This taxon was based on a single specimen (D 2140) from the Yixian Formation near Toutai, China. This specimen is broadly similar to other specimens of *Sinornithosaurus*. It possesses a rough surface of pits and ridges on the anterolateral surface of the antorbital fossa, a posteriorly bifurcated dentary, a large promaxillary fenestra with a thickened posterior rim, and many other *Sinornithosaurus millenii* autapomorphies. The eight autapomorphies provided by Lui et al. (2004) do not distinguish this specimen from any other *S. millenii* specimens.

For example, the main body of the premaxilla is longer than high in both *S. "haoiana"* and *S. millenii* (see IVPP V12811; Xu and Wu, 2001: 1741). The premaxillae in D 2140 are disarticulated and displaced. It does appear true that the anterior margin of the premaxilla is more vertical in D 2140 than in other *Sinornithosaurus* specimens, but this is variable across specimens (see IVPP V12811 and NGMC 91) and therefore may not serve as a distinguishing feature for a new species.

Contrary to Liu et al. (2004), whereas the maxillary process of the premaxilla is very long in *S. "haoiana,"* it is also long in all other specimens of *S. millenii*, and therefore the maxilla is separated from the border of the external naris (NGMC 91 and IVPP uncataloged; see fig. 20C). Liu et al. (2004) correctly note that the maxillary fenestra in D 2140 is circular and relatively small, but this cannot be used to distinguish this specimen from other *Sinornithosaurus* specimens. The maxillary fenestra is heavily damaged in the holotype skull of *Sinornithosaurus millenii*, and it is not possible to clarify this morphology in either NGMC 91 or the uncataloged IVPP specimen (fig. 23).

The last three putative synapomorphies listed by Liu et al. (2004) likewise are not sufficient to distinguish *S. "haoiana"* from *S. millenii*. The ascending process of the quadratojugal is approximately equal in length to the jugal process of the quadratojugal in *S. millenii* (~11.5 mm × ~10.5 mm, respectively). The apparently short ascending process of *S. millenii* that was depicted in the line drawing of Xu and Wu (2001: fig. 4E) does not match the much longer process in the specimen itself. Therefore, the slightly longer ascending process of the quadratojugal noted in *S. "haoiana"* is insufficient to recognize a new species. The small length:height ratio in the dentary is present in other specimens of *Sinornithosaurus* and in fact is broadly present among paravian taxa. Lastly, the pubic peduncle of the ilium in the holotype of *Sinornithosaurus* is narrower than the acetabulum just as in *S. "haoiana"* and for that matter the other microraptorine *Microraptor zhaoianus* (Hwang et al., 2002).

Thus, the reexamination of the putative synapomorphies of *Sinornithosaurus "haoiana"* reveals that they are either present in *Sinornithosaurus millenii* or variable among the number of *Sinornithosaurus* specimens. Coupled with the presence of discrete *Sinor-*

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Fig. 20. Select *Microraptor* specimens illustrating important morphological features that were thought to distinguish *M. zhaoianus* from *M. "gui."* **A,** *Microraptor "gui"* holotype IVPP V13352 with inset showing tubercle interpreted to serve as an attachment site for the biceps brachii muscle. **B,** *M. "gui"* IVPP V13325 pelvis and hindlimb showing details of the pubis and tibia. **C, D, E,** *M. zhaoianus* holotype IVPP V12330. A straight tibia can be seen in **C**; the box with asterisk is shown in more detail in **D**. Highlighted square in **D** represents possible biceps tubercle. Counterslab of **D** is shown in **E. F,** uncataloged *Microraptor* specimen housed at IVPP. **G,** *M. zhaoianus* IVPP V13320. Circles denote biceps tubercle location, arrows point to tibiae, and the stars denote the location of the pubis.

TABLE 4
Distribution of Putative *Microraptor* Species Autapomorphies among *Microraptor* Specimens

	Microraptor zhaoianus autapomorphies				*Microraptor "gui"* autapomorphies			
Specimens	no anterior serrations	basal tooth constriction	midcaudals 3 or 4 times dorsal length	accessory crest distal to lesser trochanter	prominent biceps tubercle on radius	manual digit 1 proportionally short	strongly curved pubis	bowed tibia
M. zhaoianus								
IVPP V 12330 (holotype)	**yes**	**yes**	**yes**	**yes**	?	?	? (dv)	**yes**
CAGS 20-8-001	**yes**	**yes**	**yes**	**yes**	?	?	? (dv)	no
CAGS 20-7-004	**yes**	**yes**	**yes**	?	?	?	? (dv)	no
M. "gui"								
IVPP V 13352 (holotype)	?	?	**yes**	?	**yes**	43%	**yes (ml)**	no
IVPP V 13320	?	no	**yes**	?	?	47%	? (dv)	**yes**
other *Microraptor* specimens								
IVPP V 12727	?	?	**yes**	**yes?**	?	?	?	no
IVPP V 13476	?	?	?	?	?	?	?	?
11 (2002)	?	?	**yes**	?	?	?	?	no
uncataloged 1	?	?	**yes**	?	?	44%	? (dv)	no
uncataloged 2	?	?	**yes**	?	**yes**	48%	**yes (ml)**	no
uncataloged 3	?	**yes**	**yes**	**yes**	?	?	?(dv)	no

dv = dorsoventrally compressed; ml = mediolaterally compressed.

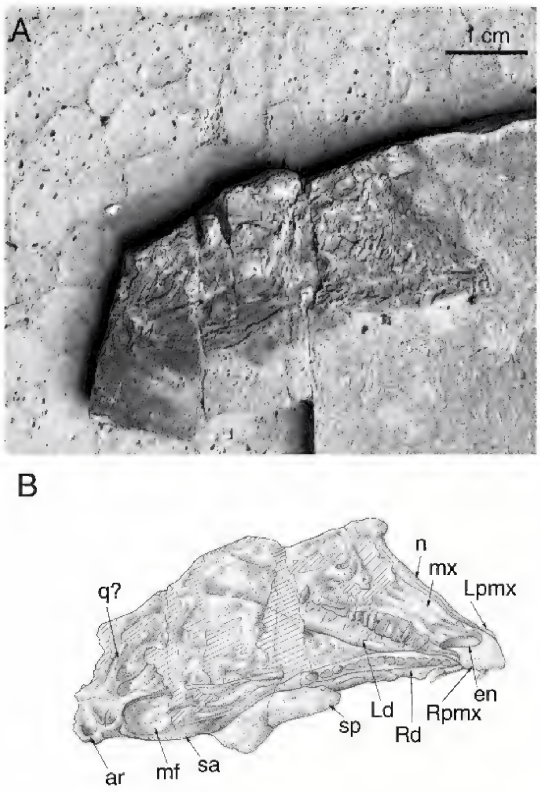


Fig. 21. Holotype skull of *Microraptor zhaoianus* (IVPP V12330). **A,** skull; **B,** interpretive line drawing adapted from Xu et al. (2000).

nithosaurus millenii autapomorphies in D 2140, we conclude that *S.* "*haoiana*" is a junior synonym of *S. millenii*.

Sinornithosaurus millenii Xu et al., 1999

Holotype: IVPP V12811.

Distribution: Early Cretaceous, Yixian Formation, Sihetun, western Liaoning, China.

Original Diagnosis: Following Xu et al. (1999: 262) and Xu and Wu (2001: 1740), a small dromaeosaurid differing from other dromaeosaurids in the presence of ornament-like pits and ridges on the anterolateral surface of the antorbital fossa; a deep excavation on the posteroventral margin of the premaxilla; a diastema between the premaxillary and maxillary teeth*; a semicircular maxillary fenestra with a straight ventral margin; a large promaxillary fenestra; the posterolateral process of the parietal long and sharply posteriorly directed; the columnlike margin of the pterygoid process of the quadrate; a large excavation on the posterolateral surface of the parasphenoid process; the bifurcated posterior margin of the dentary*; unserrated premaxillary teeth; a distinctive groove posterior to the anterior carina on the lingual surface of the

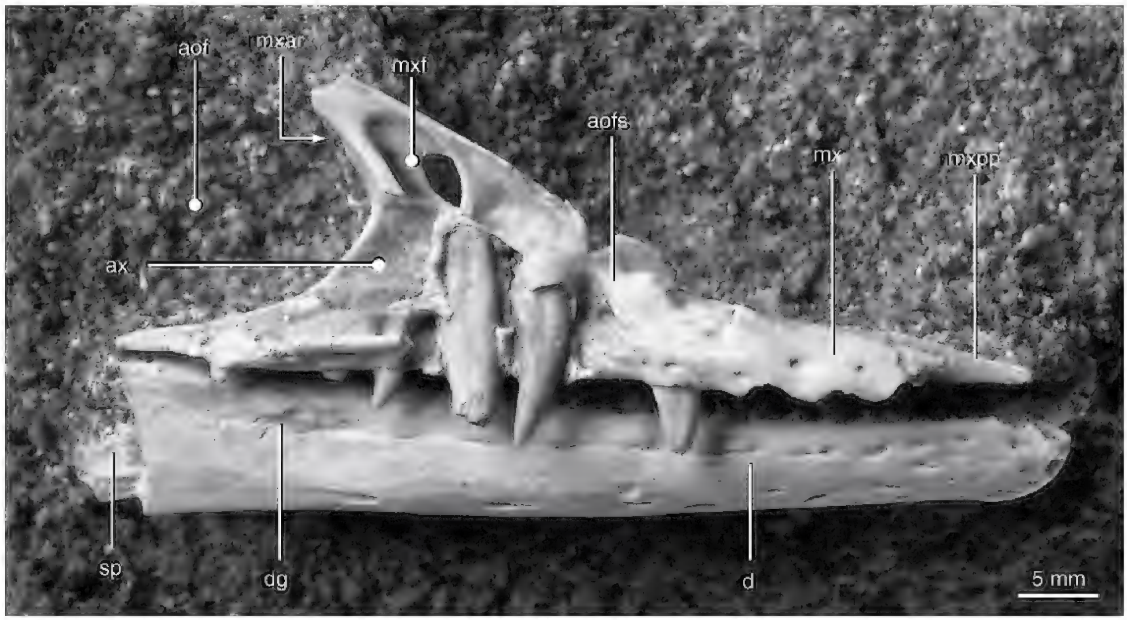
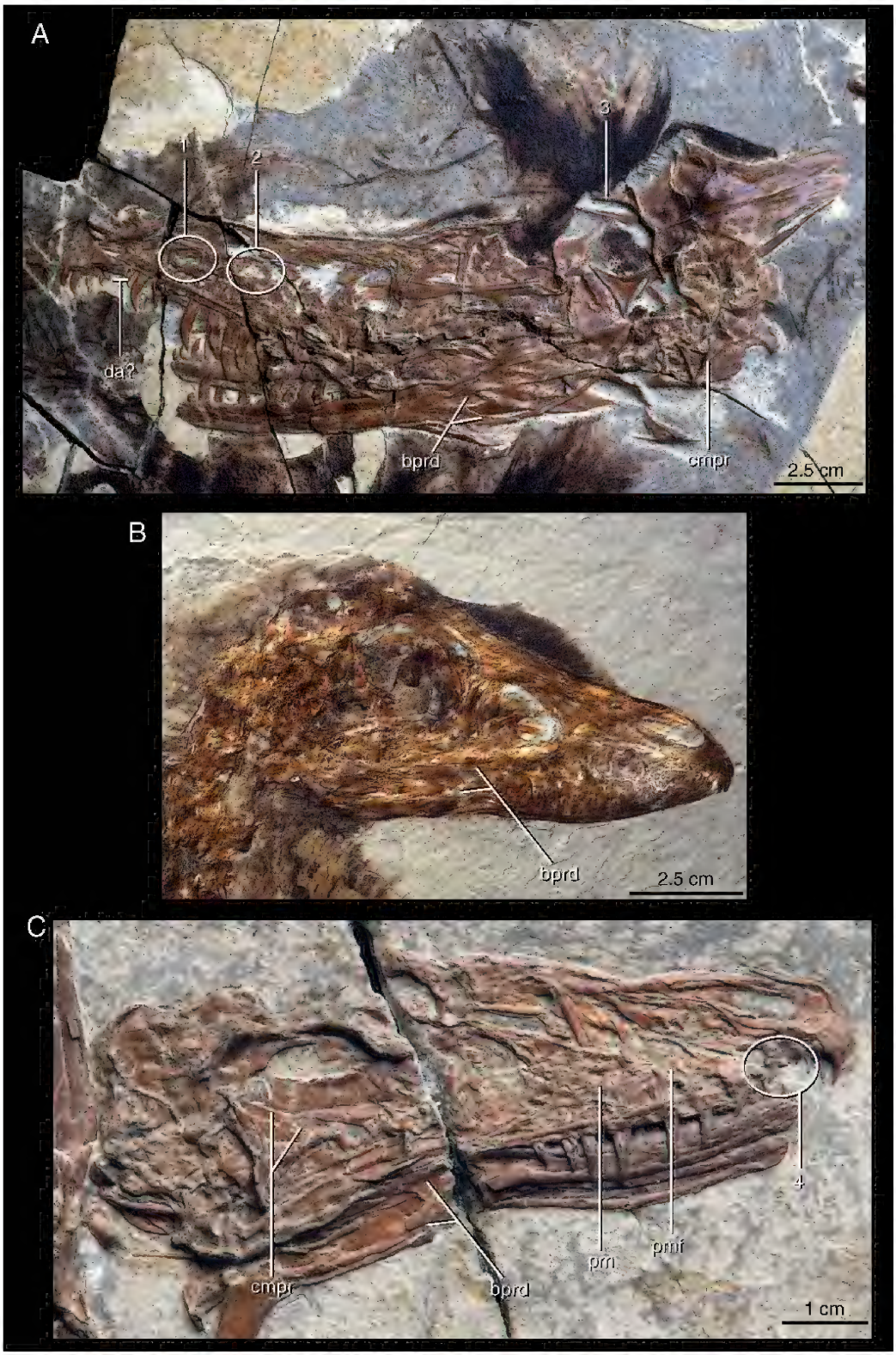


Fig. 22. Holotype of *Shanag ashile* (IGM 100/1119).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premaxillary tooth crowns; supracoracoid fenestra of coracoid; manual phalanx III-1 more than twice the length of phalanx III-2; pronounced tubercle near the midshaft of the pubis; posterodorsal process of the ischium; sub-arctometatarsalian metatarsal III.

Revised Diagnosis: A small dromaeosaurid diagnosed by the following combination of characters and autapomorphies: presence of rough surface of pits and ridges on anterolateral surface of antorbital fossa; deep excavation on posteroventral margin of premaxilla; large promaxillary fenestra with thickened posterior rim; posterolateral process of parietal long and sharply posteriorly directed; columnlike margin of pterygoid process of quadrate; large excavation on posterolateral surface of parasphenoid process (likely an anterior continuation of the basipterygoid recess); bifurcated posterior margin of dentary*; premaxillary teeth unserrated; distinctive groove posterior to anterior carina on lingual surface of premaxillary tooth crowns; supracoracoid fenestra of coracoid present; manual phalanx III-1 more than twice the length of phalanx III-2; pronounced lateral tubercle near midshaft of pubis; posterodorsal process of ischium present; partially arctometatarsalian metatarsal III (figs. 23, 24).

Discussion: *Sinornithosaurus millenii* was the first dromaeosaurid described from China and the first dromaeosaurid recognized as preserving filamentous integumentary structures. It is also one of the only Jehol theropods that were collected by professional paleontologists. In the holotype specimen (IVPP V12811) the filaments have been displaced slightly from the corresponding part of the body. Xu et al. (2001) reexamined these filamentous appendages and demonstrated that there were two distinct types of compound structures composed of multiple filaments that are unique to paravian feathers—filaments joined in a basal tuft and filaments joined at their bases in series along a central shaft. The plesiomorphic feather types further conformed to the predictions of independent developmental models of feather origins.

Xu and Wu (2001) gave a detailed treatment of the cranial anatomy of *Sinornithosaurus millenii;* however, a similarly detailed treatment of this taxon's postcranial anatomy has not been conducted. A few inconsistencies exist in the reconstruction of the skull. The quadratojugal was reconstructed as not contacting the squamosal. It was specified in the text, however, that it was unclear whether contact between these elements existed (Xu and Wu, 2001: 1745). The mandible was reconstructed as possessing a very pronounced arced profile posterior to the external mandibular fenestra. Additionally, the angular was reconstructed in an orientation nearly 45° tilted relative to the anteroposterior plane of the dentary. Such a conformation of the mandibular bones would be very odd for a dromaeosaurid. Examination of the specimen shows that the elements of the mandible are clearly disassociated and there is nothing particular about the exposed morphology of the surangular or angular that would force a distinct angle to be present in the mandible. Given this fact, plus comparisons to the mandibles of *Microraptor zhaoianus* (IVPP uncataloged) and NGMC 91, it is our view that the mandible of *Sinornithosaurus millenii* would have been dorsoventrally straight across its length.

In 2001, Ji et al. described a very well-preserved dromaeosaurid with exquisitely preserved feather integument that showed a distribution of feather types across the specimen (NGMC 91). Ji et al. (2001) noted its similarities to *Sinornithosaurus* and that some of the morphological differences were consistent with allometric changes given the smaller relative size of NGMC 91 compared

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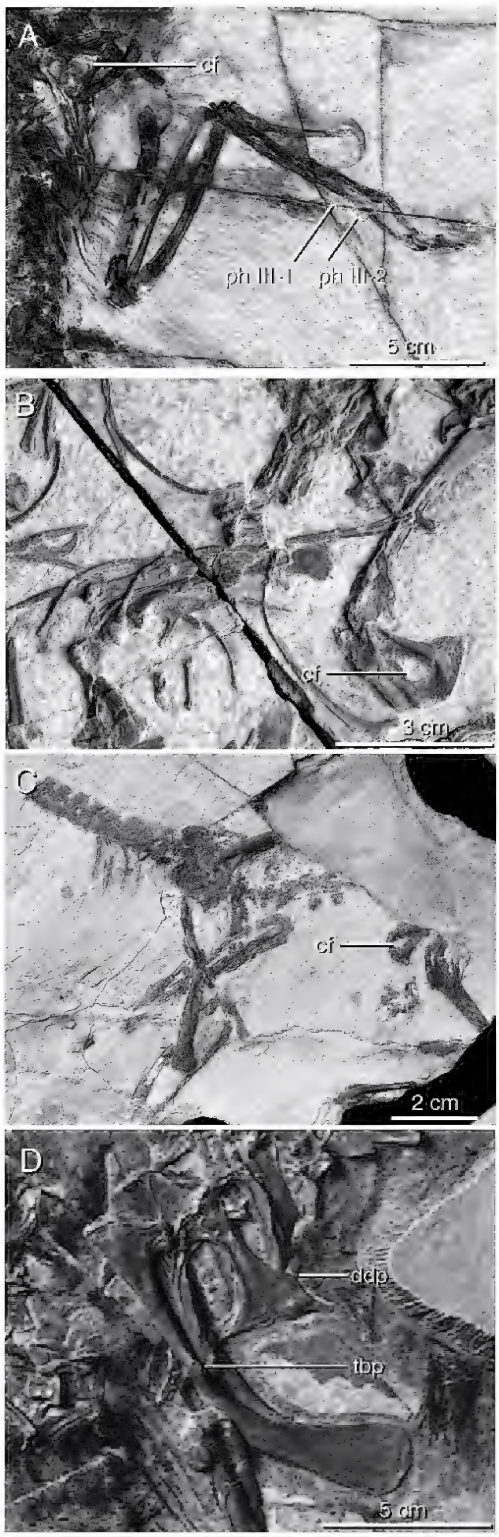
Fig. 23. Skulls of *Sinornithosaurus millenii.* **A,** holotype skull (IVPP V12811); **B,** referred specimen (NGMC 91); **C,** referred specimen (IVPP uncataloged). **1,** likely promaxillary fenestra; **2,** structure originally identified as maxillary fenestra; **3,** long and posteriorly directed lateral process of parietal; **4,** area corresponding to where a diastema should be, based on Xu and Wu (2001).



to IVPP V12811. Ji et al. (2001), citing its juvenile nature, did not erect a new taxon for NGMC 91. NGMC 91 shares a number of apomorphies with *Microraptor* and *Sinornithosaurus*. These include a coracoid fenestra, a metacarpal I plus phalanx I-1 that is shorter than metacarpal II, a radius that is less than half the width of the ulna, and a manual phalanx III-1 that is more than two times the length of manual phalanx III-2 (fig. 24). NGMC 91 cannot be referred to *Microraptor zhaoianus*, because it lacks elongate middle caudals that are three to four times the length of the dorsal vertebrae. It does possess a posteriorly bifurcated dentary, which is an apomorphy of *Sinornithosaurus* (fig. 23). For this reason, we regard NGMC 91 as a subadult specimen of *Sinornithosaurus millenii* and the scoring used for this taxon in our analysis is based both on the holotype and NGMC 91.

Two other aspects of *Sinornithosaurus millenii* anatomy are worth mentioning, the accessory antorbital fenestra and the premaxilla-maxilla diastema. In the detailed description of the holotype skeleton (IVPP V12811), Xu and Wu (2001) described the maxillary fenestra as positioned anteriorly in the antorbital fossa and possessing a straight ventral margin. The structure identified as the promaxillary fenestra was characterized as well developed and larger than the maxillary fenestra. Complicating matters is that the structure labeled as the maxillary fenestra in the line interpretation of the holotype skull is a fractured portion of the underlying right maxilla—not the structure present in the line drawing that corresponds to the maxillary fenestra in the authors' reconstruction of the skull. Examination of the holotype skull reveals that the structure that can most reliably be identified as a maxillary fenestra

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Fig. 24. Select microraptorine specimens illustrating important morphological features. **A,** forelimb of *Sinornithosaurus* (NGMC 91); **B,** uncataloged IVPP *Sinornithosaurus*; **C,** *Microraptor* (IVPP V12727); **D,** pelvis of *Sinornithosaurus* (IVPP V12811).

is in a heavily damaged area of the left maxilla (fig. 23). Therefore, any characterization of its morphology should be viewed critically. Consequently, we removed the original described maxillary fenestra morphology from the diagnosis of the taxon. Referred specimens of *Sinornithosaurus* provide little help. NGMC 91 does not have well-preserved external surfaces of the maxillae as the skull is split along the midline. The exposed right maxilla has what appears to be a dorsally displaced opening just anterior to antorbital fenestra (therefore, consistent with a maxillary fenestra), but the bone is too damaged to make a definitive identification. The presence of a promaxillary fenestra in this specimen cannot be determined. A third specimen, an uncataloged IVPP fossil, is referable to *Sinornithosaurus millenii* (fig. 20F). This specimen shows what we interpret to be the anteriorly placed, expanded promaxillary fenestra, although in this specimen the dorsal border of the fenestra is damaged and displaced partially from the main body of the maxilla. No maxillary fenestra is apparent on this specimen, but a crushed zone immediately anterior to the antorbital fenestra may be the site of the opening.

Reexamination of IVPP V12811, NGMC 91, and the uncataloged IVPP *Sinornithosaurus* specimen clarifies the nature of the premaxilla-maxilla contact in *Sinornithosaurus millenii*. Xu and Wu (2001) observed an excavation on the posterior portion of the premaxilla. The authors suggest that this excavation may be a diastema between the premaxillary and maxillary tooth rows, and they included this morphology in the diagnosis. We have chosen to remove this feature. The excavation noted by Xu and Wu (2001) is, in fact, the transition from the premaxillary body to the posterior process of the premaxilla. When placed in life articulation, the premaxillary body would have been flush with the anterior margin of the maxilla and the long posterior process of the premaxilla would have separated the body of the maxilla from the external narial opening (see NGMC 91 and uncataloged IVPP specimen) as in other dromaeosaurids. Therefore, the premaxillary tooth row would have been continuous with the maxillary tooth row, excluding the possibility of a diastema.

Sinornithosaurus has recently been the subject of some very strange speculations on a potentially venomous feeding habit (Gong et al., 2010). We find the conclusion of this paper highly suspect as have others (Gianechini et al., 2011). It is worth noting here that the long anterior maxillary teeth noted by the authors as present in *Sinornithosaurus* are clearly a preservational artifact. The anterior maxillary teeth are not apomorphically long; rather, most of the known *Sinornithosaurus* specimens have the maxillary teeth partially released from their respective alveoli (something that is common in theropod fossils). This exposes a large portion of the tooth's laterally concave root and gives the impression of long, fanglike teeth with venom-conducting grooves. Instead of venom-conducting furrows these teeth simply have the charactersic figure-eight cross-sectional teeth seen in the roots of dromaeosaurid and many other theropod teeth.

Tianyuraptor ostromi Zheng et al., 2010

Holotype: STMI-3 (fig. 25).

Distribution: Early Cretaceous, Yixian Formation, Dawangzhangzi, Lingyuan, western Liaoning, China.

Diagnosis: Following Zheng et al. (2010), "a medium-sized dromaeosaurid that differs from other dromaeosaurids in the following derived features: length of the middle caudal vertebrae more than twice that of the dorsal vertebrae, a small and extremely slender furcula, and an elongate hindlimb about three times as long as the dorsal series."

Discussion: Only a preliminary description of this taxon has been published and as a result it is poorly diagnosed. We have not had the opportunity to examine the specimen firsthand, so our observations are based on the preliminary description. Regarding the characters used to diagnose this new taxon, the elongate caudal vertebrae noted by the authors are more widely distributed, as they are present in *Microraptor*. The extremely slender furcula is interesting, but in our opinion its position along the right coracoid and right sternal plate renders its identification ambiguous. Comparison of the hindlimb length versus total dorsal series length is a bit problematic as an autapomorphy because it will be difficult to apply to new discoveries if the specimens are incomplete.

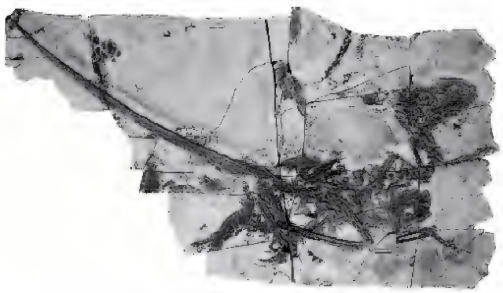


Fig. 25. Holotype of *Tianyuraptor ostromi* (from Zheng et al., 2010).

Although not mentioned in the diagnosis, the short forelimbs of *Tianyuraptor* are uncommon among dromaeosaurids (only *Austroraptor* and *Mahakala* have similarly reduced forelimbs). This feature, combined with other aspects of its morphology, suggest microraptorine affinities and lead us to consider this taxon valid but in need of a more thorough treatment of its anatomy. Prior to the present study, the phylogenetic position of *Tianyuraptor* remained unresolved, with some character data suggesting microraptorine affinities and other data placing *Tianyuraptor* closer to more derived Laurasian dromaeosaurids.

Tsaagan mangas Norell et al., 2006

Holotype: IGM 100/1015 (figs. 26, 27).

Distribution: Campanian, Djadokhta Formation, Xanadu sublocality, Ukhaa Tolgod, Ömnögov, Mongolia.

Original Diagnosis: Following Norell et al. (2006: 2), "paroccipital process pendulous and not twisted distally, basipterygoid process elongate and anteroventrally directed, maxillary fenestra large and located at the anterior edge of the antorbital fossa, jugal meets the squamosal to exclude the postorbital from the margin of the infratemporal fenestra."

Revised Diagnosis: A medium-sized dromaeosaurid diagnosed by the following combination of characters and autapomorphies: paroccipital process pendulous and not twisted distally; basipterygoid process elongate and anteroventrally directed; maxillary fenestra large and located at anterior edge of antorbital fossa*; jugal meets squamosal to exclude postorbital from margin of infratemporal fenestra; oval-shaped foramen magnum; low coracoid tuber (biceps tubercle); weak subglenoid shelf*; dorsoventrally oriented path of supracoracoid nerve through coracoid*.

Discussion: *Tsaagan mangas* was only the second dromaeosaurid taxon reported from the Djadokhta Formation since *Velociraptor mongoliensis* was described in 1924 (Osborn, 1924b). It is known from a well-preserved skull, cervical series, and partial scapulocoracoid. *Tsaagan mangas* has been included in iterations of the TWiG matrix (Norell et al., 2001, and onward) under its specimen number IGM 100/1015. In more recent versions *Tsaagan* is typically found closely related to *Velociraptor mongoliensis* and *Deinonychus antirrhopus* (Makovicky et al., 2005; Norell et al., 2006; Turner et al., 2007a, 2007b). It has been described in detail by Norell et al. (2006) and requires no more comment here.

Velociraptor mongoliensis Osborn, 1924

Holotype: AMNH FARB 6515.

Distribution: Campanian, Late Cretaceous, Djadokhta Formation, Shabarakh Usu, Mongolia.

Original Diagnosis: Following Osborn (1924b: 1–2), "skull and jaws of diminutive megalosaurian type. Cranium abbreviated; orbits greatly enlarged; face elongated; four fenestrae in the side of the cranium, one fenestra in the jaw. Teeth recurved, serrate on one or both borders, alternating in replacement; 3? + in premaxillaries, 9? + in maxillaries, 14 in dentaries. Ungual phalanges very large, laterally compressed, strongly recurved, super-raptorial in type."

Revised Diagnosis: A medium-sized dromaeosaurid diagnosed by the following combination of characters and autapomorphies (modified in part from Barsbold and Osmólska, 1999: 192): supratemporal fossa (and fenestra) subcircular, bound by laterally convex supratemporal arcade; frontal long, almost four times longer than wide across orbital portion, and almost four times as long as parietal; anterior border of internal antorbital fenestra broadly rounded; maxillary fenestra not located in a caudally open depression; premaxilla with long maxillary process reaching well beyond caudal margin of external nares; dentary very shallow, its depth constituting 1/8 to 1/7 of its length, ventral

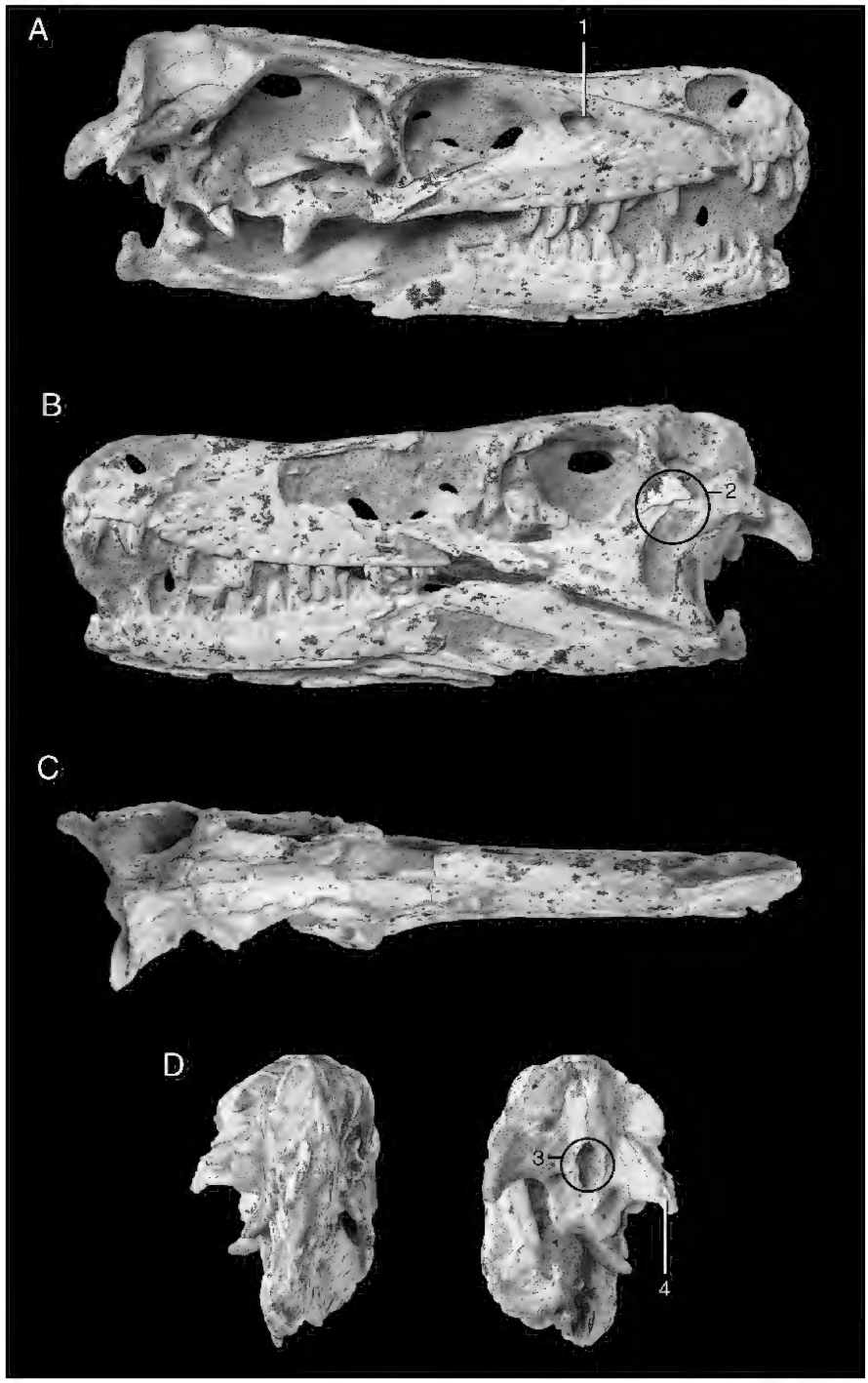


Fig. 26. Holotype skull of *Tsaagan mangas* (IGM 100/1015). **A,** right lateral view; **B,** left lateral view; **C,** dorsal view; **D,** anterior (left) and posterior (right) views. **1,** large maxillary fenestra located at the anterior edge of the antorbital fossa (char. 28.0); **2,** ascending process of jugal meets the squamosal; **3,** oval shaped foramen magnum; **4,** paroccipital process pendulous but not twisted as in other dromaeosaurids.

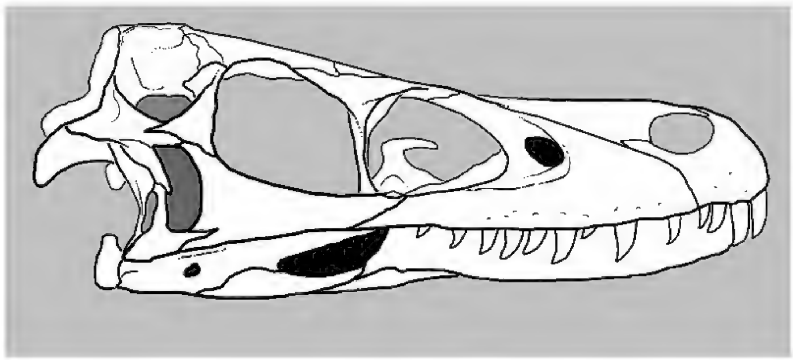


Fig. 27. Interpretive line drawing of the skull of *Tsaagan mangas*.

margin convex (dentary relatively deeper and with straight ventral margin in other dromaeosaurids); first and second premaxillary teeth larger than third and fourth; lateral wall of braincase possesses a deep prootic recess*; V-shaped furcula with reduced and asymmetrically developed hypocledium*; flangelike m. ambiens tubercle located proximally on anterior face of pubis*; well-developed anterior tuberosity proximally located on ischium* (termed the *obturator tuberosity* by Hutchinson (2001a); rounded longitudinal ischial ridge (shared with *Deinonychus antirrhopus*).

Discussion: Published shortly after the initial brief description of *Dromaeosaurus albertensis* (Matthew and Brown, 1922), *Velociraptor mongoliensis* is the second described dromaeosaurid, although at the time Osborn did not recognize its close relationship with *Dromaeosaurus*. It remains one of the best-studied species of the group, and is known from at least nine skeletons of varying levels of completeness (figs. 28, 29). It is iconic and one of the most familiar dinosaurs among nonscientists.

Barsbold and Osmólska (1999) and Norell et al. (2004) have given a detailed treatment of the cranial anatomy, whereas Norell and Makovicky (1997, 1999) have provided extensive description of postcranial anatomy. Clearly the characters given by Osborn (1924b) to diagnose this taxon are plesiomorphies and of little value now. The revised diagnosis provided above is adapted from the cranial diagnosis provided by Barsbold and Osmólska (1999) and characters noted by Norell and Makovicky (1997, 1999). A number of authors (Sues, 1977; Barsbold and Osmólska, 1999; Senter et al., 2004; Senter, 2007) have regarded *Velociraptor mongoliensis* as having depressed nasals behind the external naris or as having an "upturned" snout. As Norell et al. (2006: 7) point out, this morphology is the result of the nasals being wider anteriorly than in the midsection, so that when mediolaterally crushed, as in the holotype skull (AMNH FARB 6516) or in the "fighting dinosaur" skull (IGM 100/25), the snout has an unusual upturned appearance (fig. 29).

Velociraptor osmolskae Godefroit et al., 2008

Holotype: IMM 99NM–BYM–3/3.

Distribution: Campanian, Late Cretaceous, Bayan Mandahu Formation, Inner Mongolia, China.

Original Diagnosis: Following Godefroit et al. (2008: 433), "Long rostral plate

→

Fig. 28. Skull of "fighting dinosaur" specimen of *Velociraptor mongoliensis* (IGM 100/25) in **A,** right lateral view; **B,** left lateral view; **C,** dorsal view; **D,** posterior view. Important features of *Velociraptor* include: **1,** rounded maxillary fenestra not recessed in a depression (char. 28.1); **2,** maxillary fenestra separated from the anterior border of the antorbital fossa; **3,** a very long maxillary process of premaxilla; **4,** anterior two teeth longer than posterior two teeth; **5,** accessory depression in supratemporal fossa (char. 466.1); **6,** circular supratemporal fenestra; **7,** long nasal process of frontal.

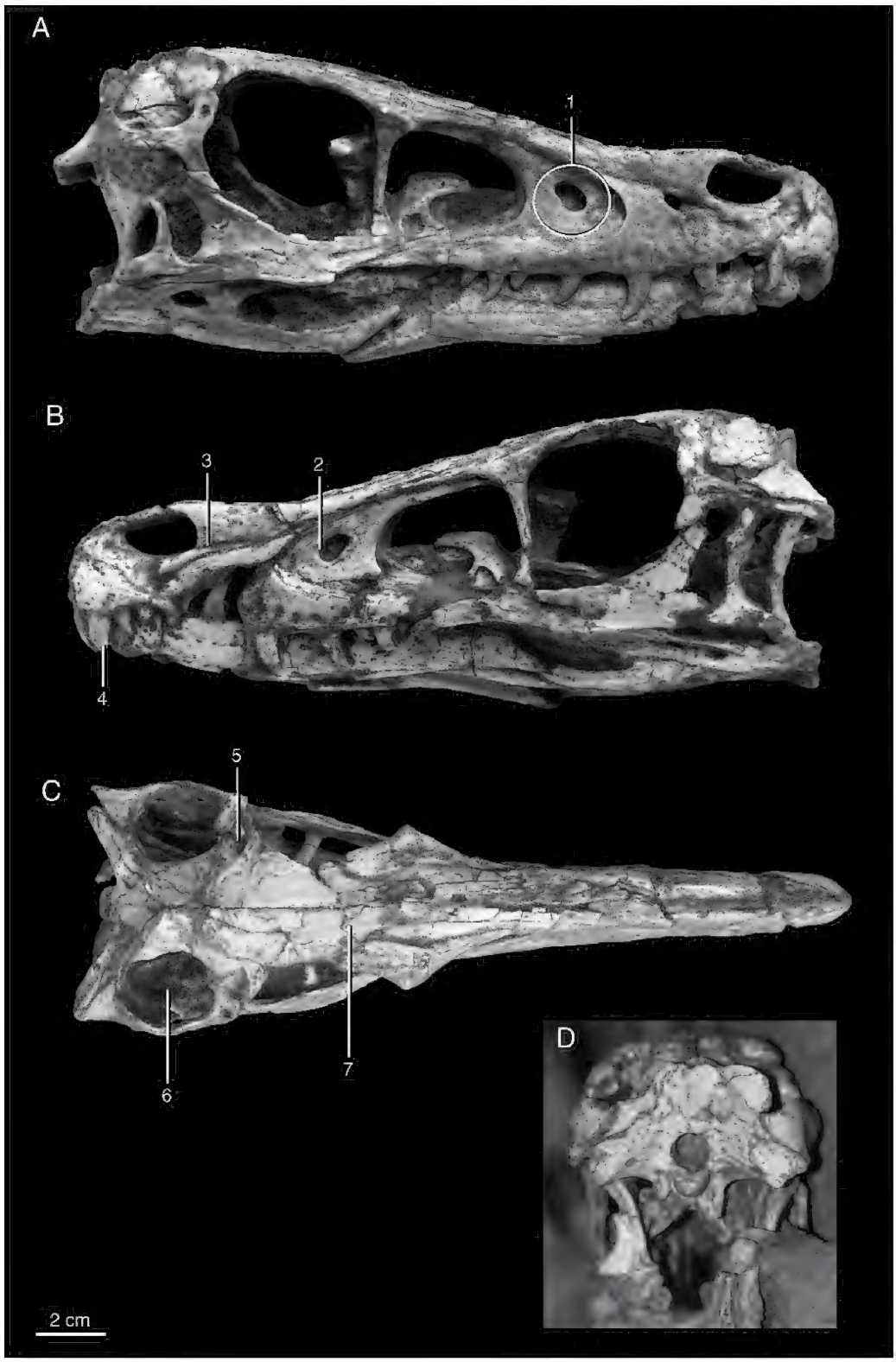

A
1
B
3
2
4
C
5
6
7
D
2 cm

Fig. 29. Lateral views of the skulls of *Velociraptor mongoliensis*: (top) holotype skull (AMNH FR 6516); (middle) IGM 100/25 (the "fighting dinosaur" skull); (bottom) IGM 100/982.

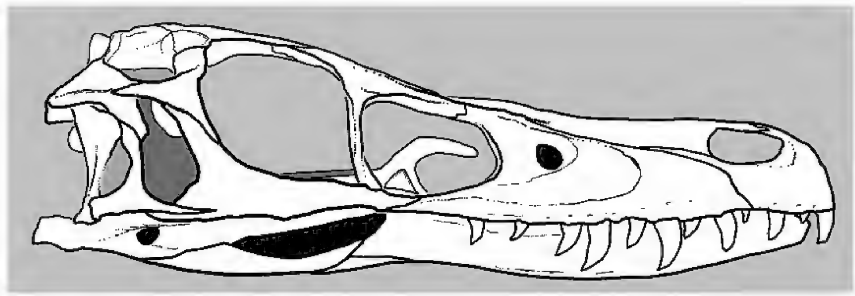


Fig. 30. Interpretive line drawing of the skull of *Velociraptor mongoliensis*.

of maxilla, with elongation index (L/H ratio) 1.38. Promaxillary fenestra subequal in size to the maxillary fenestra and teardrop shaped; long axis of the promaxillary fenestra perpendicular to the dorsal border of the maxilla; long axis of maxillary fenestra parallel to this border. Ten maxillary teeth with short unserrated carina on the apical end of the mesial edge and with incipient serrations on the distal carina."

Revised Diagnosis: A medium-sized dromaeosaurid diagnosed by the following combination of characters and autapomorphies (modified from Godefroit et al., 2008): promaxillary fenestra teardrop shaped and subequal in size to maxillary fenestra*; long axis of promaxillary fenestra perpendicular to dorsal border of maxilla; long axis of maxillary fenestra parallel to dorsal border of the maxilla.

Discussion: *Velociraptor osmolskae* is the second dromaeosaurid reported from the Djadokhta Formation–equivalent Bayan Mandahu Formation. Jerzykiewicz et al. (1993) reported the presence of *V. mongoliensis* from Bayan Mandahu, although as noted by Godefroit et al. (2008) that material has never been adequately prepared. Given this, it is possible that only a single *Velociraptor* species is present in the Bayan Mandahu Formation. Although, *V. osmolskae* is known only from paired maxillae and a lacrimal it does appear to be distinct from *V. mongoliensis*. The two species share a long facial lamina of the maxilla anterior to the antorbital fossa and a very shallow caudally open fossa surrounding the maxillary fenestra. *V. osmolskae* differs from *V. mongoliensis* in the shape and size of the maxillary and promaxillary fenestrae (as evinced by the revised diagnosis above). Although there is considerable variation in the snout morphology of *V. mongoliensis* (see Norell et al., 2006), the promaxillary fenestra is always very small in these specimens. In contrast, this fenestra is very large in *V. osmolskae* and approximates the size of the maxillary fenestra. We currently view *V. osmolskae* as valid but note the possibility that future discoveries may render it synonymous with *V. mongoliensis* as several of these pneumatic features vary considerably where large samples are known.

EUROPEAN DROMAEOSAURIDS

Balaur bondoc Csiki et al., 2010

Holotype: EME PV.313 (fig. 31).

Distribution: Maastrichtian, Late Cretaceous, Sebes Formation, Alba County, Romania.

Original Diagnosis: Following Csiki et al. (2010), a "dromaeosaurid theropod with the following autapomorphies (asterisk denotes autapomorphies unique among all theropods): hypertrophied coracoid tubercle*; sinuous ridge on lateral surface of distal humerus extends for 1/3 of the length of the bone*; prominent ridge on medial surface of distal half of humerus*; anterior surface of ulna flattened and bisected by longitudinal ridge*; fused carpometacarpus; reduced, splintlike metacarpal III*; mc III contacting mc II distally, buttressed by overhanging ridge on mc II*; distal articular surface not extending onto plantar surfaces of metacarpals I and II; manual ungual II with Y-shaped lateral and medial grooves*; phalanges of manual digit III reduced and digit nonfunctional; extremely retroverted pubes and ischia whose long axes are nearly horizontal*; pubic peduncle [of the ilium] laterally everted such that broad cuppedicus fossa faces laterally and

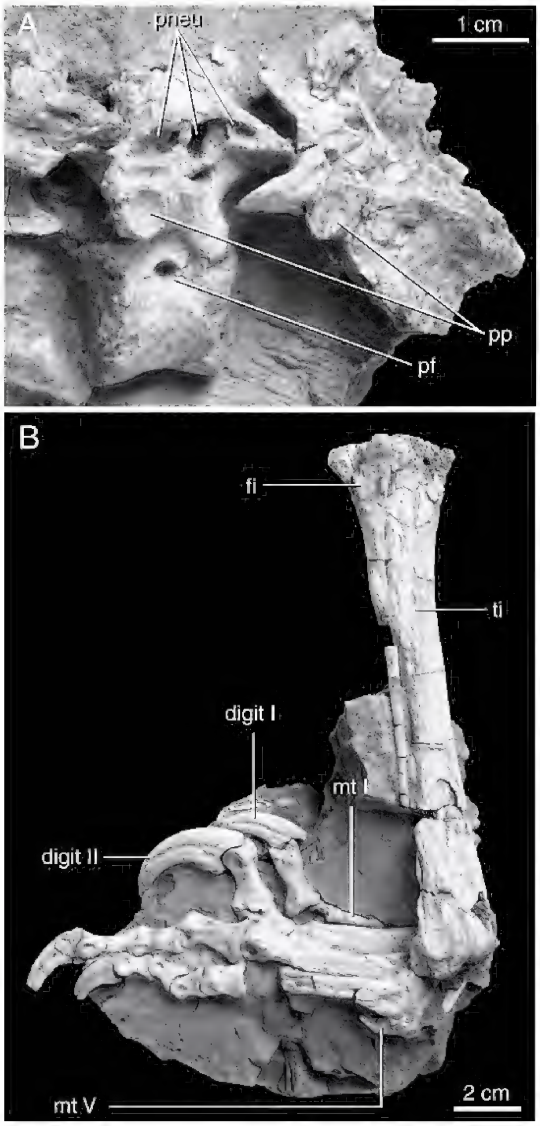


Fig. 31. Select material of *Balaur bondoc* exhibiting diagnostic features for the taxon. **A,** posterior dorsal vertebrae showing the dromaeosaurid trait of a stalked parapophysis and extensive vertebral pneumaticity; **B,** left lower leg exhibiting the derived states of a fused tibiotarsus, a fused proximal metatarsals, and a digit I modified for hyperextension.

dorsally*; pubis reoriented so that lateral surface faces ventrally and pubic tubercle located directly below acetabulum*; ischial obturator tuberosity expressed as enlarged, thin flange that contacts or nearly contacts pubis ventrally*; tarsometatarsus substantially wider (1.5×) than distal tibiotarsus*; fused metatarsus (mt II–V); robust ridges on plantar surfaces of metatarsals II–IV*; metatarsals II and III not ginglymoid; articular region of mts II–III narrower than entire distal end*; first digit of pes functional with enlarged phalanges but vestigial metatarsal I*; and short, hook-like mt V."

Discussion: This is a bizarre dromaeosaurid from the ancient European archipelago of the Late Cretaceous. The animal is perhaps most distinctive for its double sickle claw on the foot due to hypertrophy of the ungual of the first digit in addition to the typical hypertrophy of the ungual of the second digit. Csiki et al. (2010) provided an initial description of this taxon and a more detailed description of this taxon is underway (Brusatte et al., in review).

Additional details of the morphology of *Balaur* will not be discussed here, however, the description of Brusatte et al. (in review) will likely result in a modified diagnosis for *Balaur*. Some of the features included in the original diagnosis as autapomorphies appear to be more widely distributed among theropods (e.g., the reduced metacarpal III is similar to that of caenagnathids, and Y-shaped claw grooves are common to many coelurosaurs). Moreover, some of the autapomorphies identified from the shoulder girdle and pelvis many need revision in light of likely preservational distortion, initially undetected in the holotype material.

In the initial, preliminary, publication, *Balaur bondoc* was recovered as the sister taxon of the Campanian *Velociraptor mongoliensis*. This analysis was based on the dataset of Turner et al. (2007b). Future work on *Balaur* will prove important because this taxon marks the best-known European dromaeosaurid to date and has important biogeographic implications. This paper will be well illustrated and will provide adequate coverage of this important specimen.

Pyroraptor olympius Allain and Taquet, 2000

Holotype: MNHN BO001.

Distribution: Campanian-Maastrichtian, Late Cretaceous, La Boucharde, France.

ORIGINAL DIAGNOSIS: Following Allain and Taquet (2000) this taxon is diagnosed by "the presence of a deep depression on the lateral face of the ulna; a ventrally concave, distally grooved and asymmetrical metatarsal II; tooth serrations present posteriorly but restricted on the anterior carina; and an ulna that is subequal in length to metatarsal II."

REVISED DIAGNOSIS: A medium-sized dromaeosaurid diagnosed by the following combination of characters: ventrally concave metatarsal II subequal in length to ulna; tooth serrations present in posterior teeth but restricted on anterior carina.

DISCUSSION: Prior to the discovery of *Balaur bondoc*, this relatively poorly known taxon was the best-represented European dromaeosaurid (figs. 32–34). *Pyroraptor olympius* is known from Upper Campanian to Lower Maastrichtian sandstones of La Boucharde, France. The described *Pyroraptor olympius* material contains the remains of at least two individuals. The paratype of *Pyroraptor olympius* consists, in part, of a right phalanx II-2 (MNHN BO 002). Material referred to *Pyroraptor olympius* by Allain and Taquet (2000) included five "pedal phalangeal elements." It was never specified which of the associated catalog numbers (MNHN BO 006–010) pertain to which element, but one of these is an additional right phalanx II-2 that is approximately 20%–25% larger than the paratype phalanx. The two phalanges are identical in all respects save that the larger phalanx has a more mediolaterally robust flexor heel that is not as medially displaced nor as ventrally extensive as in the smaller MNHN BO 002. Also referred to *Pyroraptor olympius* was a dorsal vertebra (MNHN BO 017). This vertebra is a bit atypical for a dromaeosaurid, although it is incomplete and poorly preserved. Most of the vertebral centrum is either distorted or unpreserved. The neural spine is not as squared off in lateral view as other dromaeosaurids such as *Velociraptor* and it cannot be determined whether the spine expanded into a spine table dorsally as in other dromaeosaurids (Norell and Makovicky, 1999). Additionally, the prezygapophyses slant dorsomedially more strongly than in other dromaeosaurids and the parapophyses are not preserved in MNHN BO 017 so that it can be determined whether they are "stalked" or pedicellate as in other dromaeosaurids.

Additional undescribed *Pyroraptor* remains include the distal portion of a right metatarsal III (MNHN uncataloged) and a nearly complete (left?) metatarsal I (this element appears to have been referred to *Pyroraptor* as a partial distal end of metacarpal I, MNHN BO 012).

The deep depression on the lateral surface of the ulna noted by Allain and Taquet (2000) as a diagnostic feature is a preservational artifact (fig. 33). The deep depression sits within a larger, shallower depression. In this depression concentric compression fractures are apparent both near the deepest portion of the depression and along the extremities. Although a distinct depression may have indeed been present, given the apparent preservational distortion, this character should not be used to diagnose this taxon.

A distally grooved and asymmetric metatarsal II is characteristic of dromaeosaurids in general (Ostrom, 1969a) and not a unique character of *Pyroraptor olympius*. Furthermore, tooth serrations present on the posterior carina, but absent on the anterior carina, is widespread among dromaeosaurids. The exceptions are *Dromaeosaurus albertensis* and *Achillobator giganticus* where serrations are present on both carinae and *Buitreraptor gonzalezorum* where serrations are absent on both carinae. Therefore, this character is diagnostic for a much more inclusive clade (probably Dromaeosauridae) and is not unique to *Pyroraptor olympius*.

It is clear that *Pyroraptor olympius* is a dromaeosaurid, however, at present it is hard to adequately diagnose this taxon based on clear apomorphies. Many of the characteristics proposed by Allain and Taquet (2000) prove to be widespread among dromaeosaurids. Two characteristics remain as possible apomorphies or what may serve as a unique combination of characters, namely metatarsal II ventrally concave and subequal to the length of the ulna. These features may prove sufficient to refer any future material to this taxon at which point a more detailed diagnosis may be possible.

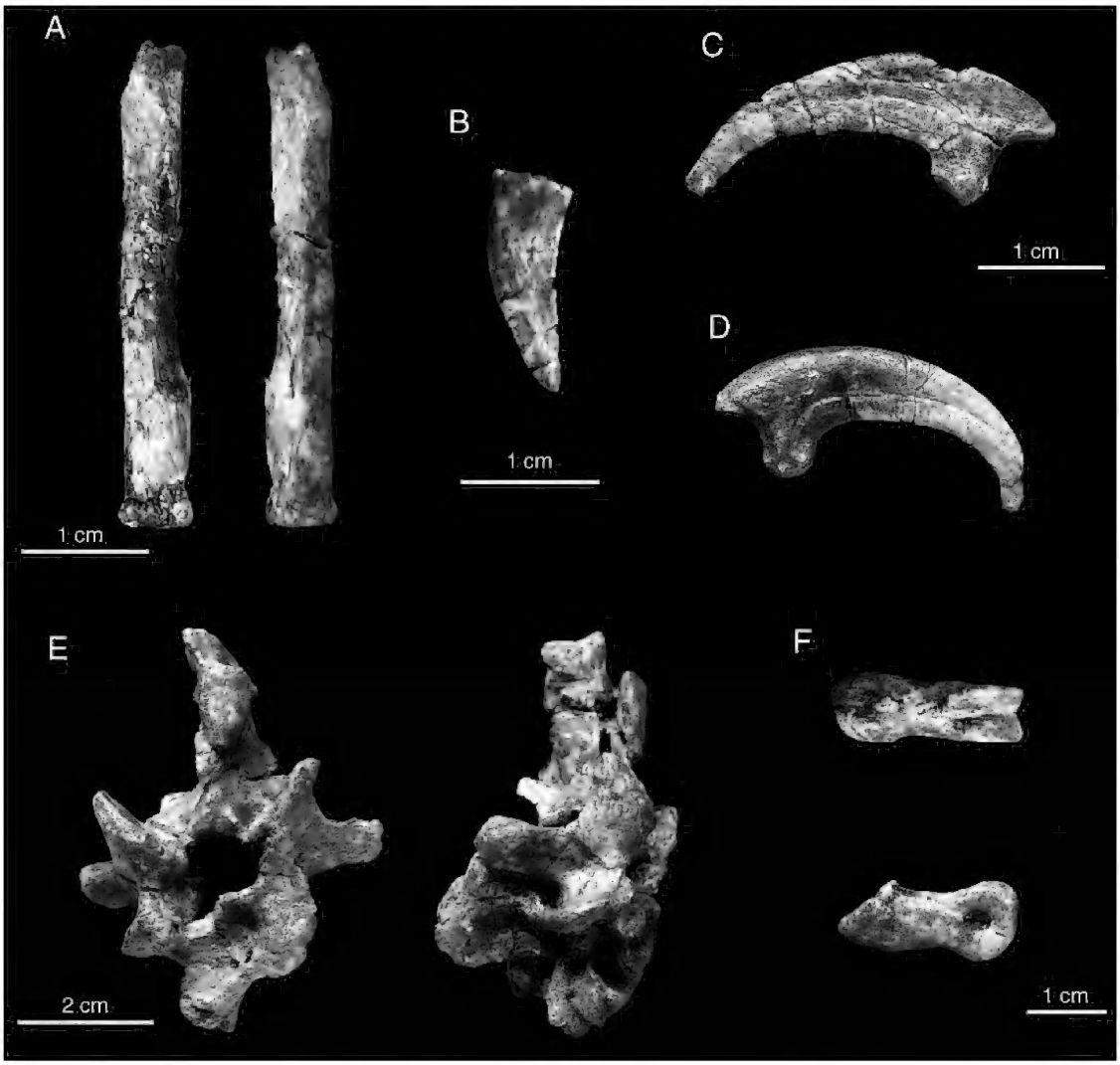


Fig. 32. Select material of *Pyroraptor olympius*. **A,** manual phalanx (MNHN BO 011); **B,** tooth; **C,** ungual phalanx of pedal digit II; **D,** holotype specimen, ungual phalanx of pedal digit II (MNHN BO 001); **E,** dorsal vertebra (MNHN BO 017); **F,** phalanx II-2.

Variraptor mechinorum LeLoeuff and Buffetaut, 1998

Holotype: MDE-D168.

Distribution: Late Campanian to Early Maastrichtian, Late Cretaceous, Grès à Reptiles Formation, La Bastide Neuve.

Original Diagnosis: Following Le-Loeuff and Buffetaut (1998: 106), "the cervico-dorsal vertebrae have prominent epipophy[ses] and [well] developed[ed] hypapophysis; the cervico-dorsals bear two pleurocoels; the cervico-dorsals to the last dorsal bear a hyposphene-hypantrum articulation; the centra shorten from the anterior to the posterior dorsals; the sacrum consists of five coossified sacral vertebrae; the sacrocaudal vertebra has a trapezoidal centrum; the transverse processes of the sacrocaudal are aliform; the humerus has a well-developed deltopectoral crest and internal tubercle and also bears a strongly developed medial tubercle."

Revised Diagnosis: Not applicable. This taxon is here considered a nomen dubium.

Fig. 33. Forelimb elements of *Pyroraptor olympius*, ulna (MNHN BO 004) and radius (MNHN BO 013). Arrow indicates the preservational artifact initial interpreted as a unique depression.

DISCUSSION: LeLoeuff and Buffetaut (1998) based *Variraptor mechinorum* on isolated and extremely poorly preserved remains from two separate localities from southern France. The holotype consists of an incomplete and badly crushed posterior dorsal vertebra and sacrum. These elements preserve no characters diagnostic of Dromaeosauridae, or other less inclusive clades of coelurosaurs. The unassociated referred material includes a right humerus, a cervicodorsal vertebra, a posterior dorsal vertebra, and a femur. This material was used by the authors to augment the description and diagnosis of *Variraptor*.

Like the holotype material, the referred specimens lack specific apomorphies diagnostic of Dromaeosauridae. The cervicodorsal vertebra has a well-developed hypapophysis and is thus referable only to Maniraptora. Allain and Taquet (2000) noted the nondiagnostic nature of the *Variraptor mechinorum* holotype and concluded that the taxon is a nomen dubium. We agree with Allain and Taquet (2000) and follow their interpretation.

NORTH AMERICAN DROMAEOSAURIDS

ATROCIRAPTOR MARSHALLI CURRIE AND VARRICCHIO, 2004

HOLOTYPE: TMP 95.166.1 (fig. 35).

DISTRIBUTION: Late Campanian or Early Maastrichtian, Horseshoe Canyon Formation, Drumheller, Alberta.

ORIGINAL DIAGNOSIS: Following Currie and Varricchio (2004: 115), a "small velociraptorine, dromaeosaurid theropod that differs from *Saurornitholestes* and *Velociraptor* in having a shorter, deeper face. Subnarial body of premaxilla is taller than its anteroposterior length as in *Deinonychus* and possibly *Dromaeosaurus*. Internarial and maxillary processes of premaxilla subparallel and oriented more dorsally than posteriorly. Larger maxillary fenestra than in any other velociraptorine. Maxillary fenestra is directly above the promaxillary fenestra, rather than well behind it as in all other dromaeosaurids. Maxillary teeth more strongly inclined toward the throat than in all other dromaeosaurids except *Bambiraptor* and *Deinonychus*. Maxillary dentition is essentially isodont."

REVISED DIAGNOSIS: *Atrociraptor marshalli* is a small dromaeosaurid that cannot currently be diagnosed with autapomorphies, but it is sufficiently characterized by a (currently) unique combination of characters: proportionally short and dorsoventrally high maxilla; body of premaxilla longer than tall (shared with *Deinonychus*); nasal and maxillary processes of premaxilla strongly slanted dorsally (shared with *Deinonychus*); maxillary fenestra placed close to anterior margin of antorbital fossa (shared with *Achillobator*, *Tsaagan*, and *Dromaeosaurus*) and located dorsal to promaxillary fenestra; maxillary teeth strongly inclined posteriorly (shared with *Bambiraptor* and *Deinonychus*).

DISCUSSION: This fragmentary taxon was recovered from the upper Campanian or lower Maastrichtian Horseshoe Canyon Formation of Alberta, Canada, in 1995 and given a brief description by Currie and Varricchio (2004). *Atrociraptor* consists of

Fig. 34. Right metatarsal elements of *Pyroraptor olympius*. **A,** right metatarsal II (MNHN BO 003) in medial view; **B,** right metatarsal II (MNHN BO 003) in posterior view; **C,** right metatarsal III in anterior view. Arrow indicates the concave posterior margin of metatarsal II characteristic of *Pyroraptor*.

partial premaxillae, the right maxilla, right dentary, fragmentary left dentary, teeth, and several bone fragments. Currie and Varricchio (2004) referred to this taxon as a "small velociraptorine" with a short, deep face. The teeth are strongly inclined caudally, a trait it shares with *Bambiraptor feinbergorum* and *Deinonychus antirrhopus*.

To date *Atrociraptor marshalli* has been included in only three phylogenetic analysis—the one conducted by Currie and Varricchio (2004) based on 42 characters, the analysis of Senter (2007), and most recently in an analysis by Longrich and Currie (2009). Currie and Varricchio (2004) recovered a single fully resolved most parsimonious cladogram with *Atrociraptor* as the sister taxon of *Deinonychus*, with *Dromaeosaurus* the basalmost dromaeosaurid. Senter (2007) found *Atrociraptor* as the sister taxon of a clade composed of *Achillobator*, *Dromaeosaurus*, and *Utahraptor*. Longrich and Currie (2009) recovered *Atrociraptor* as part of a clade that also include *Saurornitholestes* and *Bambiraptor*, which they dubbed Saurornitholestinae. As these results are highly disparate, no consensus exists regarding the affinities of *Atrociraptor* to other dromaeosaurids.

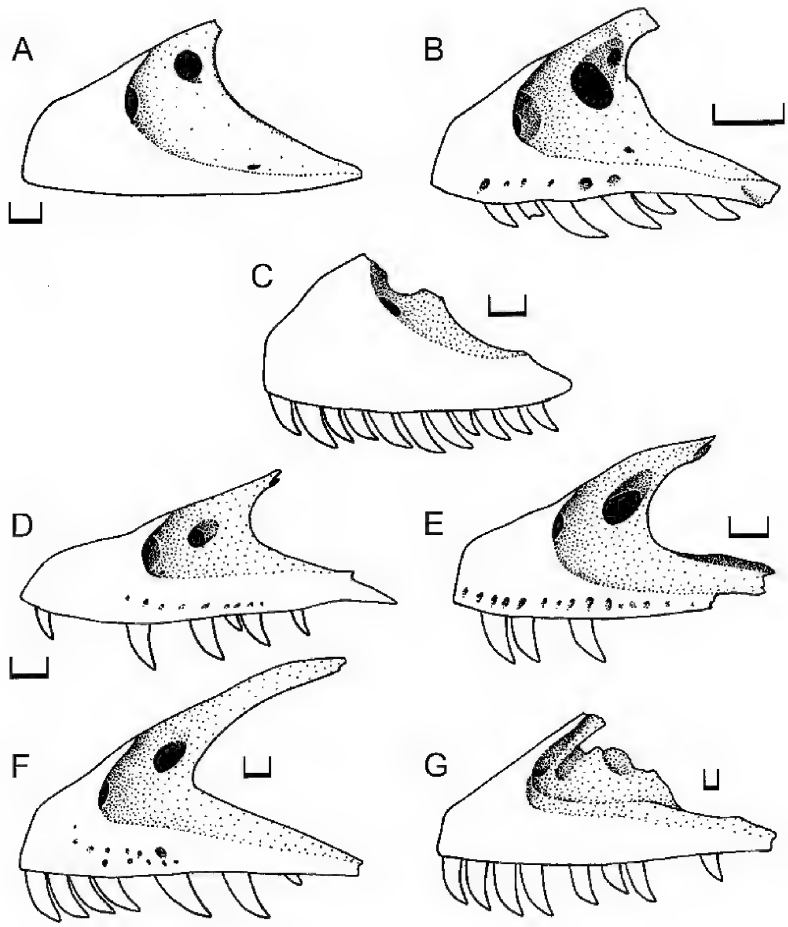


Fig. 35. The rostral area of a variety of dromaeosaurids. **A,** cf. *Bambiraptor feinbergorum* (MOR 553S-7.30.91.274); **B,** *Bambiraptor feinbergorum* (AMNH FR 30556); **C,** *Atrociraptor marshalli* (TMP 95.166.1), reversed image of right maxilla; **D,** *Velociraptor mongoliensis* (IGM 100/25); **E,** *Saurornitholestes langstoni* (TMP 94.12.844), reversed image of right maxilla; **F,** *Deinonychus antirrhopus* (YPM 5232); **G,** *Achillobator giganticus* (MNUFR 15). Reproduced from Currie and Varrichio (2004: 120).

The position of the maxillary fenestra in *Atrociraptor marshalli* is near the rostral boundary of the antorbital fossa. It is difficult to tell because the dorsal margin of the maxilla right above the maxillary fenestra is broken, but the location appears to be similar to the extreme anterior placement of the maxillary fenestra in *Tsaagan mangas* (IGM 100/1015).

Bambiraptor feinbergorum (Burnham et al., 2000)

Holotype: AMNH FARB 30556.

Distribution: Mid to late Campanian, Late Cretaceous, Two Medicine Formation, Montana.

Original Diagnosis: Following Burnham et al (2004), "jugal with row of foramina along ventral margin; scapula with large, medially directed acromion; distinct, short scapulocoracoid suture; coracoid with neck or peduncle forming part of glenoid; coracoid foramen absent; 13 dentary teeth, nine maxillary teeth; ratio of humerus plus ulna to femur large; pubis with distal shaft and boot rotated posterodorsally; ischium with small proximal dorsal process; femur strongly recurved laterally and posteriorly.

Revised Diagnosis: Provisional, awaiting future descriptive work on both *Bambiraptor* and *Saurornitholestes*. The only difference between *Bambiraptor* and *Saurornitholestes* is

the proportional length of the frontal, which is longer in *Bambiraptor* than in *Saurornitholestes*.

DISCUSSION: *Bambiraptor feinbergorum* is quite small (less than a meter long) and generally regarded as a juvenile to subadult (Burnham, 2004; Currie and Varricchio, 2004; Norell and Makovicky, 2004). Burnham et al. (2000) based this taxon on a relatively complete and well-preserved skeleton from the middle to late Campanian Two Medicine Formation of Montana and gave it a preliminary description. A longer description was later provided by Burnham (2004) with attempts at functional interpretation regarding some of the taxon's anatomy.

Unfortunately, this later description is not very detailed and the author misidentified portions of the morphology present in the holotype. For instance, the correct sides for the nasals and quadratojugals were misidentified. Additionally, two of the supposedly diagnostic characters for the taxon—coracoid foramen absent and coracoid with a constricted neck proximally—were the results of misinterpretation of the preserved element. Both the left and right coracoids are damaged proximally giving the appearance that the blade of the coracoid is constricted proximally. When the crushing and damage of the element are accounted for it is similar to other basal paravian coracoids. Also, the coracoid foramen is only apparently absent because of damage to the coracoid. The "notched" proximal surface is in fact part of the medial wall of the n. supracoracoideus foramen.

In a number of respects *Bambiraptor* presents a complex history. When first reported, it was referred to *Velociraptor* (Burnham et al., 1997) with Feduccia (1999) figuring and briefly discussing aspects of its morphology. Later, Burnham et al. (2000) erected a new taxon, *Bambiraptor feinbergi*, for the material. However, *Bambiraptor feinbergi* is very similar to the nearly contemporaneous *Saurornitholestes langstoni* (Sues, 1978) and the two taxa differ only slightly in regard to the amount of frontal participation in the orbit. As noted by Norell and Makovicky (2004) this trait could potentially vary ontogenetically.

Moreover, as originally named by Burnham et al. (2000) the specific epithet for this taxon was "*feinbergi.*" However, as the etymology of this name was in honor of two individuals, the correct spelling should be "*feinbergorum.*" The taxonomic list of dromaeosaurids given in *The Dinosauria* (Norell and Makovicky, 2004) follows this and refers to the specific epithet as "*feinbergorum.*"

Lastly, confusion exists over the proper collection numbers for the holotype and referred material. When first described *Bambiraptor feinbergorum* was exhibited at the Florida Institute of Paleontology, Graves Museum of Archaeology and Natural History. As such it received a FIP number, with the holotype receiving the initial accession number (FIP 001) and the referred material receiving the successive numbers (FIP 002–036). The American Museum of Natural History was later gifted with the material referred to *Bambiraptor*. In Burnham's (2004) more detailed description he references the holotype of *Bambiraptor feinbergorum* as AMNH 001 (as does Makovicky et al., 2005) and the referred material as AMNH 002-036. However, no such numbers exist for *Bambiraptor*, with the holotype instead reposited as AMNH FARB 30556. It should also be noted that Norell et al. (2006) and Turner et al. (2007a) erroneously referred to the holotype as "AMNH FARB 30554."

Currently, *Bambiraptor* has been included in only three phylogenetic analyses—Currie and Varricchio (2004), Senter et al. (2004), and Longrich and Currie (2009). Currie and Varricchio (2004) included only six dromaeosaurid taxa and a supraspecific Troodontidae as the ingroup and recovered a single most parsimonious tree. In this case, *Bambiraptor* was recovered as the sister taxon to an *Atrociraptor* + *Deinonychus* clade supported by posteriorly directed maxillary teeth (40-1), and an anterior ramus of the maxilla that is shorter anteroposteriorly than dorsoventrally (20-1). Senter et al. (2004) and Senter (2007) recovered *Bambiraptor* as the sister taxon to a clade composed of *Microraptor* + *Sinornithosaurus*. This was supported by four unambiguous synapomorphies—a proximally constricted coracoid, manual phalanx III-1 greater than or equal to twice the length of

phalanx III-2, manual phalanx I-1 bowed, and metatarsal V greater than or equal to 1/2 the length of metatarsal IV. The characters supporting this grouping are problematic. As discussed above, the constricted coracoid is a preservational artifact. *Bambiraptor* does have a dorsoventrally "bowed" or arched manual phalanx I-1. However, the supposedly "bowed" manual phalanx I-1 in *Microraptor zhaoianus* is ambiguous at best and in fact appears to be a preservational artifact owing to the two-dimensional nature of the specimens. *Sinornithosaurus millenii* (NGMC 91) may have bowed I-1 phalanges, but this too is complicated by two-dimensional preservation.

There is a possibility that *Bambiraptor* is a juvenile specimen of *Saurornitholestes* (Burnham et al., 2000; Norell and Makovicky, 2004). As noted by Norell and Makovicky (2004) and discussed below, *Saurornitholestes langstoni* currently lacks an adequate diagnosis. The original diagnosis proposed by Sues (1978) is not useful as it is based almost entirely on plesiomorphies. A precise estimate of the ontogenetic age of *Bambiraptor* has proven difficult because of remodeling of the fibula (personal obs.). A clear resolution of whether *Bambiraptor feinbergorum* is synonymous with *Saurornitholestes* necessitates detailed treatment of material known for each of these taxa. A confounding factor with *Bambiraptor* is that it may at least partially be based on a chimera, given that there are three identically sized tibiae included in the type specimen. Nevertheless, we are currently of a mind to provisionally regard both *Saurornitholestes* and *Bambiraptor* as valid until future work can resolve this issue.

Deinonychus antirrhopus Ostrom, 1969

Holotype: YPM 2505 (fig. 36).

Distribution: Late Aptian or Early Albian, Cloverly Formation, Montana.

Original Diagnosis: Following Ostrom (1969a: 12), "a small, bipedal theropod with a moderately large head, moderately long and well-developed hind limbs, fore limbs elongate, manus long and slender in construction. Pes of medium length with four digits, the fifth represented by a vestigial metatarsal. Digital formula 2-3-4-5-0. Digits III and IV subequal in length, II specialized and bearing a very large, trenchant and strongly recurved ungual, I reduced and directed backward. Pes functionally didactyl (III and IV). Distal end of metatarsal II deeply grooved; metatarsal II not greatly compressed proximally. Articular facets of II developed to permit unusual extension but very limited flexion between first and second phalanges. Manus with three very long digits (formula 2-3-4), digits IV and V lost. Metacarpal I short and irregular in shape. Metacarpal III long, slender and divergent from II. Carpus consists of radiale and ulnare only. Radiale with well-defined asymmetrical ginglymus proximally for articulation with radius. Humerus and radius-ulna not reduced. Skull with large, subcircular to oval orbits and three antorbital fenestrae. Supraorbital rugosities on postorbital and lachrymal. Preorbital bar slender and in weak contact with a thin, platelike jugal. Quadratojugal very small, T-shaped, and apparently not in contact with squamosal. Nasals long, narrow, and unfused. Inferior premaxillary process forms lower margin of external naris. Pterygoid very long and slender, ectopterygoid complex and pocketed ventrally. Palatine expanded, with subsidiary palatine fenestra medially. Fifteen maxillary teeth, four asymmetrical, subincisiform premaxillary teeth, 16 subisodont dentary teeth. All teeth with anterior and posterior serrations; denticles of posterior serrations nearly twice as large as denticles of anterior serrations on all teeth. Twenty-two or 23 presacral vertebrae, 3 or 4 sacrals and approximately 40 caudals. Cervical vertebrae of moderate length, massive, platycoelous, and sharply angled. Dorsals short, and platycoelous. All caudals except the first 8 or 9 bear extremely long (up to 10 segments), rodlike, prezygapophyseal processes. Chevrons also elongated into long, paired, double bony rods extending forward beneath the preceding 8 or 9 segments. Ischium with triangular obturator process. Pubis (if correctly identified) short and greatly expanded into a subcircular, scoop-shaped element, with a distinct obturator foramen."

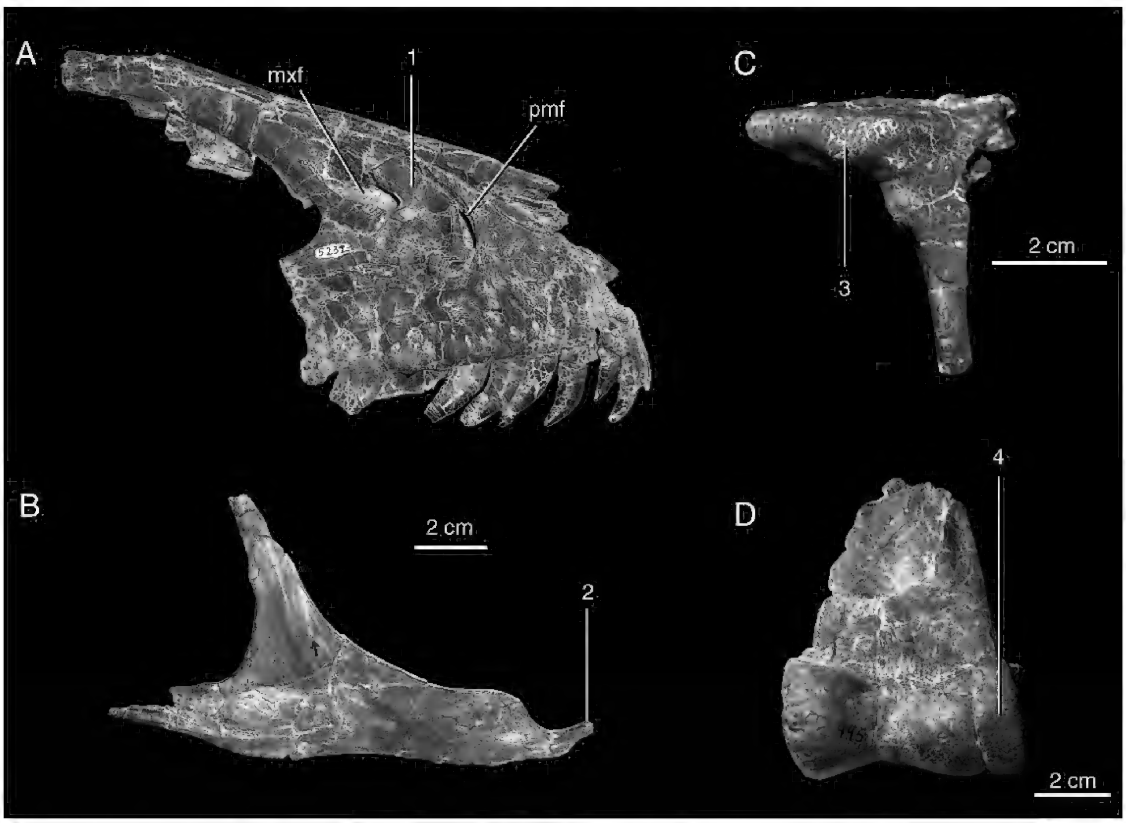


Fig. 36. Select skull remains of *Deinonychus antirrhopus*. **A,** right maxilla (YPM 5232) in lateral view; **B,** left jugal (YPM 5210) in medial view; **C,** right lacrimal in lateral view; **D,** left astragalocalcaneum (YPM 5226) in anterior view. Important features of *Deinonychus antirrhopus* include: **1,** a maxillary fenestra located dorsal to the level of the promaxillary fenestra; **2,** lobate anteriormost process of jugal beneath antorbital fenestra; **3,** a very prominent lacrimal boss; **4,** a large and wide calcaneum.

Revised Diagnosis: A large dromaeosaurid diagnosed by the following combination of characters and autapomorphies: 15 maxillary teeth; four asymmetrical, subincisiform premaxillary teeth; 16 nearly isodont dentary teeth; all teeth with anterior and posterior serrations; denticles of posterior serrations nearly twice as large as denticles of anterior serrations on all teeth; lobate anteriormost process of jugal beneath antorbital fenestra*; lacrimal boss prominent; prefrontal greatly reduced*; maxillary fenestra located dorsal to level of promaxillary fenestra; large, wide calcaneum.

Discussion: This taxon is the best-known North American dromaeosaurids and is represented by multiple individuals from several localities. The original diagnosis for this taxon, however, is comprised of plesiomorphic characteristics. Ostrom (1969a) based this taxon on a number of specimens preserving elements from across the entire body, although at the time a braincase was lacking. These characters were assayed from multiple individuals, as the type specimen was accumulated in a multi-individual bonebed. This material was recovered from the Lower Cretaceous Cloverly Formation of Montana. It is currently known from at least eight articulated and disarticulated skeletons and skulls, which includes the partial skeleton and braincase from the Antlers Formation of Oklahoma (Brinkman et al., 1998) (fig. 37). The Antlers Formation material was referred to *Deinonychus antirrhopus* based on postcranial similarity and the presence of posterior serrations on all teeth that are twice as large as the anterior

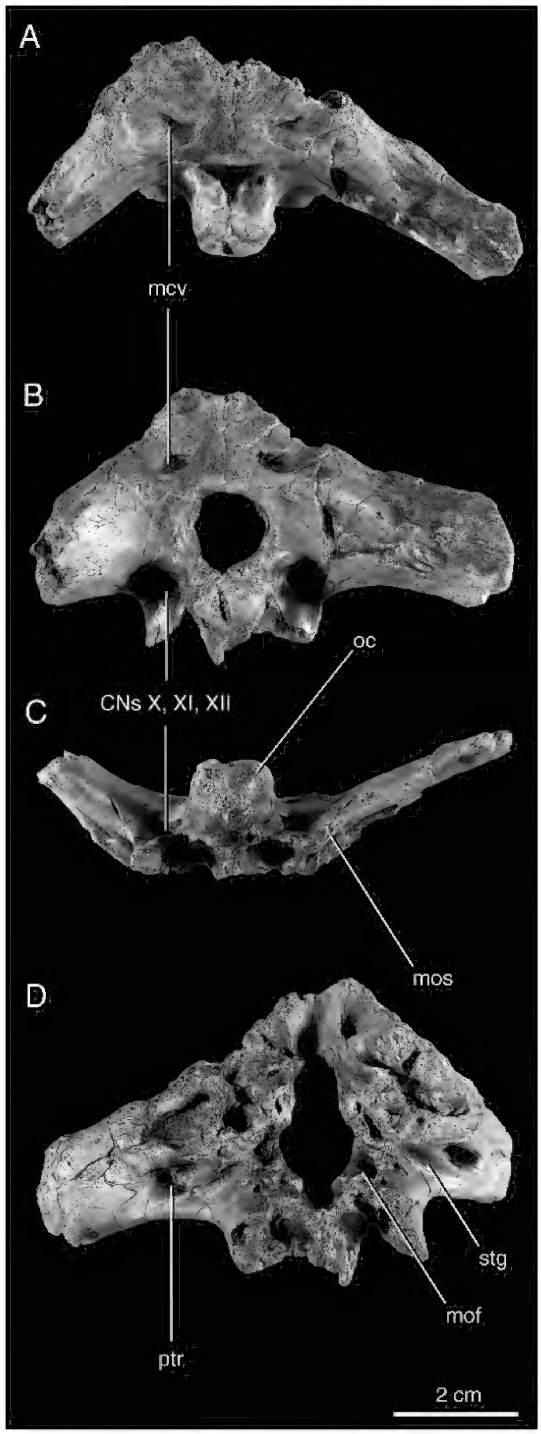


Fig. 37. Braincase of *Deinonychus antirrhopus* (OMNH 50268). **A,** dorsal view; **B,** posterior view; **C,** ventral view; **D,** anterior view.

serrations (identified here as one of the autapomorphies of this species). The age of the Antlers Formation remains poorly constrained relative to the Cloverly Formation. It is possible that future additional material or analysis of the Antlers taxon could reveal it to be taxonomically distinct from *Deinonychus antirrhopus*.

The osteology of *Deinonychus* was given extensive treatment by Ostrom (1969a, 1969b, 1974, 1976a). Maxwell and Witmer (1996) and Witmer and Maxwell (1996) provided a brief description of additional cranial remains. This, plus the additional material discussed above, was examined for scoring *Deinonychus* in the present study.

Currie and Varricchio (2004) recovered *Deinonychus antirrhopus* as derived within dromaeosaurids, as the sister taxon of *Atrociraptor marshalli*. This was supported by one unambiguous synapomorphy—a premaxilla with a subnarial depth that is higher than long (30-1). In that analysis, *Deinonychus* and *Atrociraptor* also shared with *Bambiraptor* maxillary teeth that are strongly inclined posteroventrally (40-1). Senter et al. (2004) and Currie and Varricchio (2004) have only six dromaeosaurid taxa in common in their analyses. Senter et al. (2004) recover *Bambiraptor* well outside the least inclusive clade containing *Deinonychus*, and *Dromaeosaurus* was recovered closer to *Deinonychus* than in the analysis of Currie and Varricchio (2004). Senter et al. (2004) recover *Deinonychus* as the sister taxon of an *Achillobator* + (*Utahraptor* + *Dromaeosaurus*) clade. This relationship is supported by a single unambiguous synapomorphy; "dentary straight" (25-0). However, the robustness of this putative synapomorphy is highly suspect. Of the four taxa, only *Deinonychus* is scored as possessing character state 25-0—it is coded as 25-1 in *Achillobator* and as unknown (?) in *Dromaeosaurus* and *Utahraptor*. However, the known specimen of *Achillobator* lacks a dentary, so this character state cannot be considered anything other than uncertain (?). This leaves *Deinonychus* as the only taxon in the group to exhibit the putative synapomorphy. Therefore, it is equally parsimonious to interpret a straight dentary as autapomorphic for *Deinonychus*, with this conclusion the only one supported by the current data.

In the phylogenetic analyses of Xu et al. (2002a), Hwang et al. (2002), and Xu and Norell (2004), *Deinonychus* was recovered in a clade with *Dromaeosaurus* and *Achillobator* when the largely incompletely scored *Adasaurus* was removed from the analysis. This clade was unambiguously supported by the presence of D-shaped premaxillary teeth (unknown in *Achillobator*) and a loss of opisthopuby (unknown in *Dromaeosaurus*) (Norell and Makovicky, 2004). The scoring of the latter trait was based on the reconstruction offered by Ostrom (1974), but further examination of MCZ 4371 indicates the pubis was more reverted than in Ostrom's reconstruction.

Dromaeosaurus albertensis Matthew and Brown, 1922

Holotype: AMNH FARB 5356 (figs. 38–41).

Distribution: Campanian, Oldman Formation, Alberta, Canada.

Original Diagnosis: Following Colbert and Russell (1969: 40), "skull moderate length and height. Rugosity present on dorsolateral rim of lacrimal. Orbit circular, larger than first antorbital fenestra. Supratemporal arcade long. Quadratomandibular articulation slightly depressed. Pterygoid wing of palatine narrow. Dental formula: four premaxillary, nine maxillary, 11 dentary teeth. Anterior carina of maxillary and dentary teeth displaced medially near base of crown. Sixteen denticles per 5 mm on anterior and posterior carinae. Pes similar to that of *Deinonychus*, but with relatively shorter phalanges."

Revised Diagnosis: A medium-sized dromaeosaurid diagnosed by the following combination of characters and autapomorphies (modified in part from Currie, 1995: 577): nine maxillary teeth; anterior carina of maxillary or dentary tooth close to midline of tooth near tip, twists toward lingual surface*; premaxilla deeper and thicker than other dromaeosaurids; quadratojugal stout; tip of frontal flatter and margin of supratemporal fossa less pronounced; postorbital process of frontal sharply demarcated from the dorsomedial orbital margin; posteromedial process of palatine slender; anterior and posterior tooth denticles subequal in size; anteroposterior short lateral lamina of maxilla anterior to antorbital fossa; nasals with V-shaped suture posteriorly between frontals; deep notches anteriorly on frontal for articulation with lacrimal; presence of either an enlarged promaxillary fenestra or an extremely anteroventrally placed maxillary fenestra with no promaxillary fenestra depending on interpretation of identity of opening; dorsal tympanic recess very weakly expressed; moderately developed preotic pendant; expression of anterior tympanic recess and/or basipterygoid recess absent on the basisphenoid or basipterygoid processes*.

Discussion: A preliminary description of this dromaeosaurid was presented by Matthew and Brown (1922) based on partially prepared material recovered by Barnum Brown from the Upper Cretaceous Oldman Formation of Alberta Canada. The type (AMNH FARB 5356) is based on a partial skull with lower jaws, hyoids, associated pedal elements, and a left metacarpal I. Colbert and Russell (1969) gave *Dromaeosaurus albertensis* a more thorough and complete description while Currie (1995), after repreparation of the holotype and CT analysis, was able to add new information on cranial and braincase morphology and improve upon the incorrect reconstruction of the skull by Colbert and Russell (1969).

Apart from the holotype, few other specimens of *Dromaeosaurus albertensis* exist. These include an isolated frontal (NMC 12349; Sues, 1978), a partial dentary (Currie, 1987), and numerous isolated teeth (Currie et al., 1990), all of which are difficult to definitively refer to the type. *Dromaeosaurus* appears to be distinct from other dromaeosaurids based on the general lack of pneumaticity in the braincase (only the caudal tympanic recess is present) and maxillary/dentary teeth carinae that curve lingually. The anterior and posterior semicircular canals in *Dromaeosaurus albertensis* (AMNH FARB 5356) are oriented largely in the vertical plane whereas those of *Velociraptor mongoliensis* (Norell et al., 2004; IGM 100/982) and *Tsaagan mangas* (Norell et al., 2006) are rotated more posteriorly. Scorings in this analysis are based entirely on the holotype material (AMNH FARB 5356). Furthermore, we have interpreted the preserved

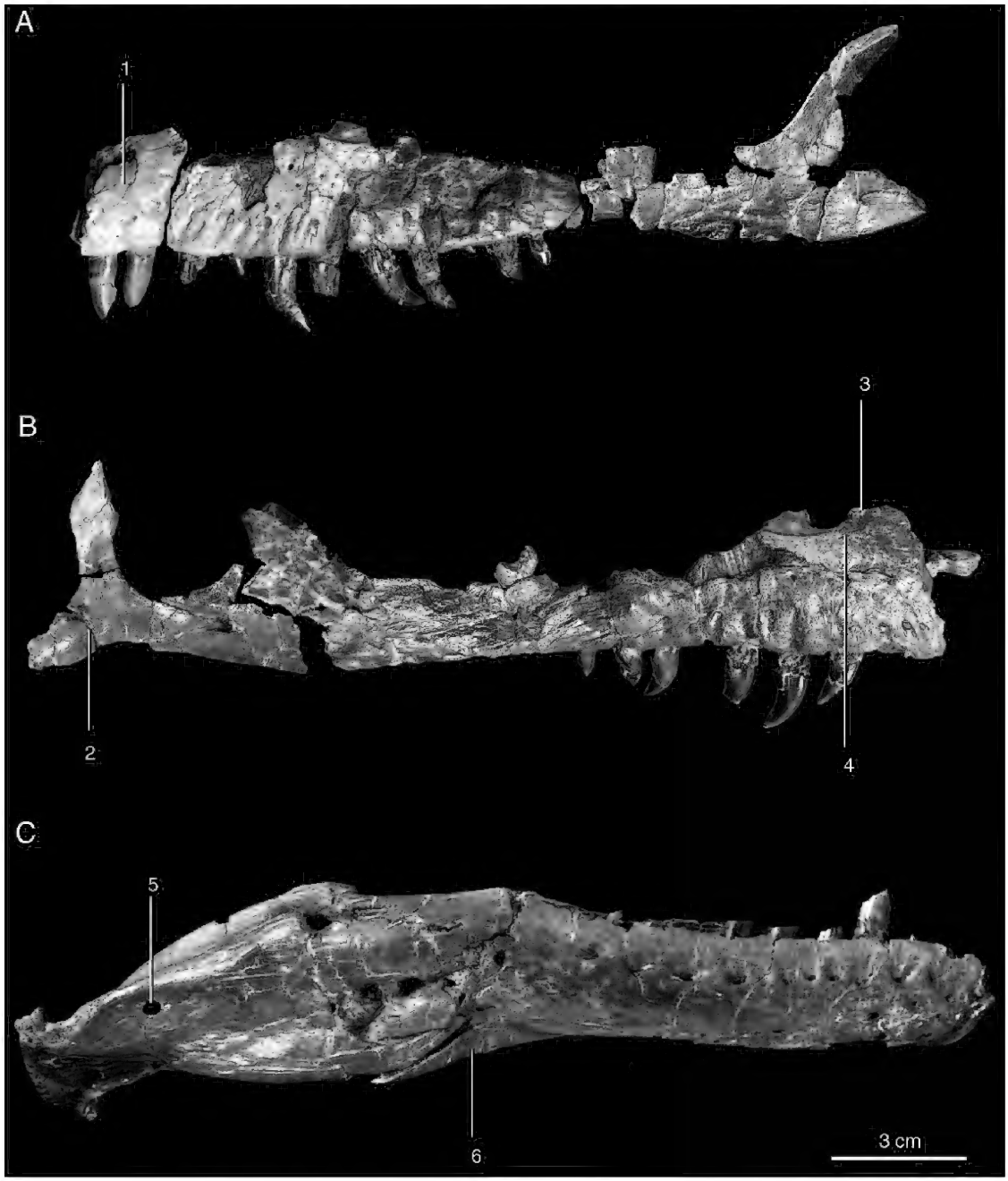
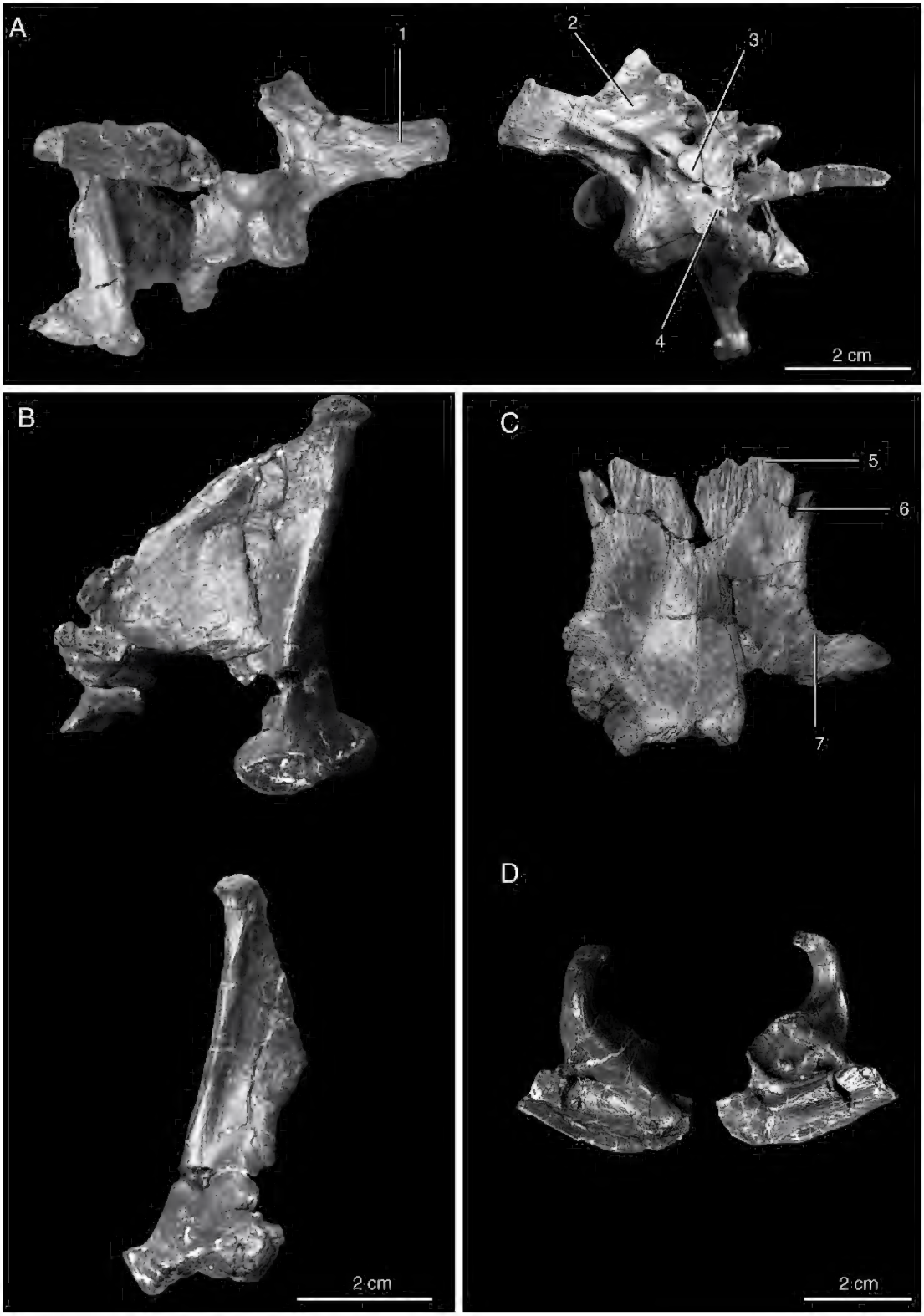


Fig. 38. Rostrum of *Dromaeosaurus albertensis* (AMNH FARB 5356). **A,** left premaxilla, maxilla, and jugal in lateral view; **B,** right maxilla, jugal, and quadratojugal in lateral view; **C,** right mandible in lateral view. Important features of *Dromaeosaurus albertensis* include: **1,** a deep and thickened premaxilla; **2,** a stout quadratojugal; **3,** anteroposterior short lateral lamina of the maxilla anterior to the antorbital fossa; **4,** presence of either an enlarged promaxillary fenestra or an extremely anteroventrally placed maxillary fenestra with no promaxillary fenestra depending on interpretation of identity of opening; **5,** presence of a distinct surangular foramen (char. 74.1)—a deinonychosaurian synapomorphy; **6,** a laterally exposed splenial (char. 75.1)—a deinonychosaurian synapomorphy.


A
1
2
3
4
2 cm
B
2 cm
C
5
6
7
D
2 cm

fenestra in the maxilla as a promaxillary fenestra. Changing the interpretation of this feature does not effect the placement of *Dromaeosaurus* within Dromaeosauridae.

Currie and Varricchio (2004) recovered *Dromaeosaurus* as the basalmost dromaeosaurid in their analysis, while Senter et al. (2004) recovered *Dromaeosaurus* as the most derived. Senter et al. (2004) groups *Dromaeosaurus* with *Utahraptor* as sister taxa based on one unambiguous synapomorphy—mesial and distal keels of posterior teeth with an equal number of denticles per 5 mm (20-0). In the analyses of Xu et al. (2002a), Hwang et al. (2002), and Xu and Norell (2004), *Dromaeosaurus* is recovered in a clade with *Deinonychus* and *Achillobator* when *Adasaurus* is excluded from the analysis. This clade is unambiguously supported by the presence of D-shaped premaxillary teeth (unknown in *Achillobator*) and a loss of opisthopuby (unknown in *Dromaeosaurus*) (Norell and Makovicky, 2004). In more current versions of the TWiG dataset (Novas and Pol, 2005; Makovicky et al., 2005; Norell et al., 2006; Turner et al., 2007a, 2007b) and variants thereof (Longrich and Currie, 2009), *Dromaeosaurus albertensis* groups in an unresolved clade containing *Achillobator giganticus*, *Utahraptor ostrommaysorum,* and *Adasaurus mongoliensis*.

Hesperonychus elizabethae Longrich and Currie, 2009

Holotype: UALVP 48778.

Distribution: Campanian, Dinosaur Park Formation, Dinosaur Provincial Park, Canada.

Diagnosis: Following Longrich and Currie (2009: 5003), "pubic peduncle of ilium with medial surface deeply excavated; posterior wing of ilium with medial shelf split to form anterior posterior processes*; lateral tubercles of pubis wing-like and curving anteriorly*; pubic apron shifted onto posterior surface of pubis; pubic symphysis teardrop-shaped in lateral view; ischiadic process of pubis reduced to a narrow lamina."

Discussion: This small dromaeosaurid is known from a single incomplete pelvic girdle and isolated referred pedal elements. Nevertheless, the morphology of the pelvis is convincingly microraptorine in aspect, an observation that is borne out by the phylogenetic analysis of Longrich and Currie (2009). *Hesperonychus*, like other microraptorines, has a pubis that curves posteriorly bending sharply beginning midshaft, a spatulate pubic symphysis, and a large lateral process roughly midway down the shaft of the pubis. The discovery of a Late Cretaceous North American microraptorine is significant for a number of reasons. *Hesperonychus* extends the temporal range of Microraptorinae by almost 45 million years and suggests a remarkable level of morphological conservatism within this dromaeosaurid subclade. Additionally, the presence of this taxon in North America is perhaps unexpected, but results in a significant geographic range extension and substantiates a more complex biogeographic interaction between Asia and western North America. With the great similarity between the Late Cretaceous faunas of western North America and Asia, and the dense sampling record in the Late Cretaceous it is perhaps more surprising that a Late Cretaceous microraptorine has not been found in Asia.

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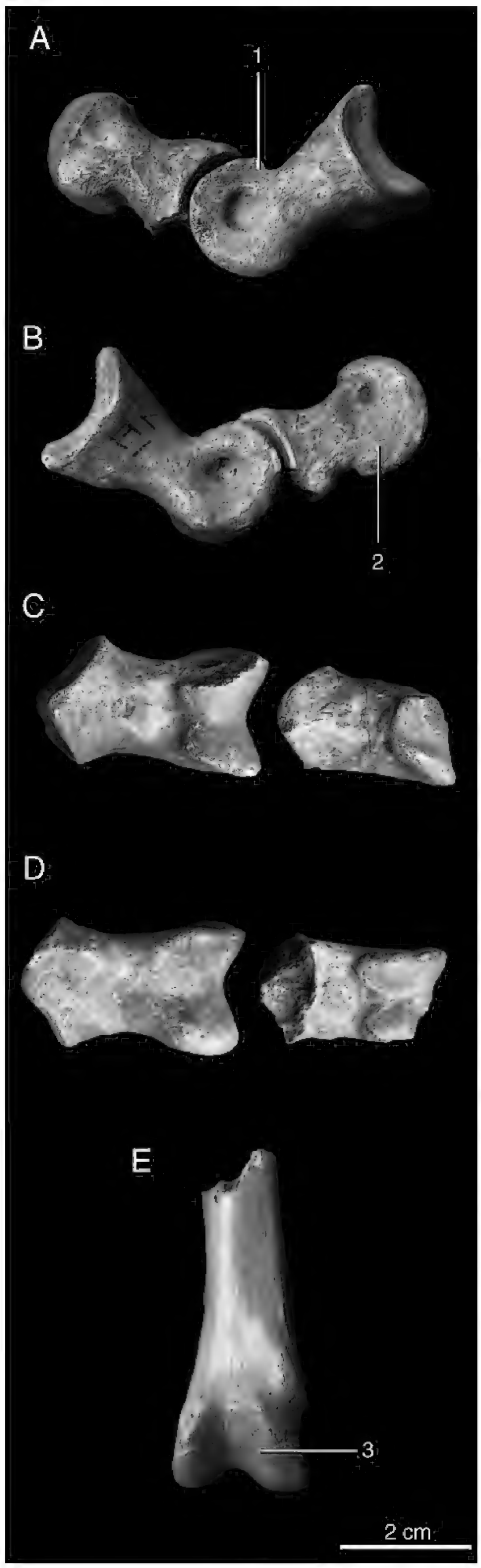
Fig. 39. Select skull remains of *Dromaeosaurus albertensis* (AMNH FARB 5356). **A,** braincase in posterior and right lateral views; **B,** left quadrate in medial and posterior views; **C,** frontal in dorsal view; **D,** left ectopterygoid in dorsal and ventral views. Important features of *Dromaeosaurus albertensis* include: **1,** paroccipital process elongate and slender with parallel dorsal and ventral edges (char. 56.0), which distally curves ventrally becoming pendant (char. 57.1); **2,** a very weakly expressed dorsal tympanic recess; **3,** prominent preotic pendent; **4,** expression of the anterior tympanic recess or basipterygoid recess absent on the basisphenoid or basipterygoid processes; **5,** tip of frontal flat; **6,** deep notches anteriorly on frontal for articulation with lacrimal; **7,** postorbital process of frontal more sharply demarcated from the dorsomedial orbital margin.



SAURORNITHOLESTES LANGSTONI SUES, 1978

HOLOTYPE: TMP 74.10.5.

DISTRIBUTION: Campanian (Judithian), Judith River Formation, Dinosaur Provincial Park, south-central Alberta, Canada.

ORIGINAL DIAGNOSIS: Following Sues (1978: 383), "a very small, lightly built theropod. Frontal triangular, not basined between the median suture and the orbital rim. Posterior part of the frontal well rounded and slightly inflated, without frontoparietal crest. Lateral walls of the anterior part of the endocranial cavity flaring laterally. Ectopterygoid complex, pocketed ventrally. Teeth with well-developed denticles (24–26 per 5 mm) on posterior carinae and tiny denticles (c. 35 per 5 mm) on anterior carinae."

REVISED DIAGNOSIS: Awaiting detailed description of unpublished material.

DISCUSSION: *Saurornitholestes langstoni* has been reported from the Oldman Formation, Alberta (Sues, 1978), the Judith River Formation, Montana (Russell, 1969), Dinosaur Park Formation, Alberta (Currie, 2005), Kirtland Formation, New Mexico (Sullivan and Lucas, 2000), the Aguja Formation, Texas (Sankey, 2001), and the Prince Creek Formation, Alaska (Fiorillo and Gangloff, 2000). Sullivan (2006) has subsequently referred the Kirtland Formation material to a new species of *Saurornitholestes* (see below).

As noted by Norell and Makovicky (2004), *Saurornitholestes langstoni* has not had definite diagnostic characters proposed to support it. The original diagnosis proposed by Sues (1978), is not useful as it is based almost entirely on plesiomorphy. The anterior denticle morphology and spacing (5 to 6 denticles/

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Fig. 40. Preserved left second pedal elements and metatarsal of *Dromaeosaurus albertensis* (AMNH FARB 5356). **A,** phalanges II-1 and II-2 in medial view; **B,** phalanges II-1 and II-2 in lateral view; **C,** phalanges II-1 and II-2 in dorsal view; **D,** phalanges II-1 and II-2 in ventral view; **E,** metatarsal II in anterior view. Important features of *Dromaeosaurus albertensis* include: **1,** a modified phalanx II-1; **2,** modified phalanx II-2 for hyperextension of the ungual (char. 204.1); **3,** ginglymoid articulation on metatarsal II (char. 201.1)—a deinonychosaur synapomorphy.

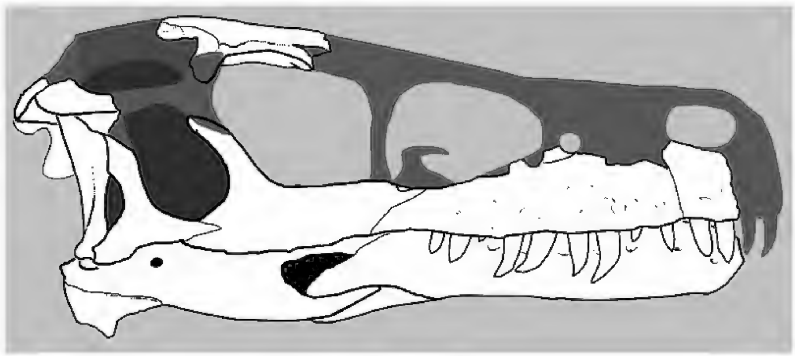


Fig. 41. Interpretive line drawing of the skull of *Dromaeosaurus albertensis*.

mm), however, seems to be effective in referring isolated teeth to *Saurornitholestes* (Sankey, 2001; Sankey et al., 2002). Currie and Varricchio (2004) recently described a maxilla for *Saurornitholestes langstoni* (TMP 94.12.844). Additional postcranial material awaits further description (TMP 67.20.36, TMP 88.121.39, MOR 660). Our view from the totality of the published and unpublished material is that *Saurornitholestes langstoni* is a valid taxon. Scorings in this analysis are based on the holotype, published descriptions, and examination of the unpublished TMP and MOR osteological specimens. Recent work (Zanno et al., in press) has drawn into question the unambiguous referral of teeth to *Saurornitholestes* and *Dromaeosaurus*.

Currie (1995) considered *Saurornitholestes* as a close *Velociraptor* relative. Makovicky et al. (2003) and Novas and Pol (2005) found the phylogenetic position of *Saurornitholestes langstoni* to be very labile among dromaeosaurids more derived than *Sinornithosaurus* and *Microraptor*. Norell et al. (2006) and Turner et al. (2007a) found *Saurornitholestes* in an unresolved position but still more derived than microraptorines. Makovicky et al. (2005) recovered *Saurornitholestes langstoni* in a clade with *Achillobator giganticus*, *Dromaeosaurus albertensis*, *Utahraptor ostrommaysorum*, and *Adasaurus mongoliensis*. Senter (2007) recovered a similarly composed clade including *Atrociraptor marshalli*. Turner et al. (2007b) found a phylogenetic position for *Saurornitholestes langstoni* most similar to that envisioned by Currie (1995)—in a clade with *Tsaagan mangas*, *Velociraptor mongoliensis*, and *Deinonychus antirrhopus*. In contrast, Longrich and Currie (2009) recovered *Saurornitholestes* in a clade with the North American taxa *Atrociraptor* and *Bambiraptor*.

Saurornitholestes robustus Sullivan, 2006

Holotype: SMP VP-1955.

Distribution: Campanian, Late Cretaceous, De-na-zin Member of the Kirtland Formation, San Juan Basin, New Mexico.

Original Diagnosis: Following Sullivan (2006: 253), "a species of *Saurornitholestes* distinguished from *Saurornitholestes langstoni* by its larger and more robust frontal (twice as thick)."

Revised Diagnosis: Not applicable. This taxon is here considered a nomen dubium.

Discussion: The frontal described by Sullivan (2006) is extremely weathered and damaged. It lacks synapomorphies of *Saurornitholestes* and even fails to preserve synapomorphies of Dromaeosauridae (e.g., the postorbital process is damaged; therefore, it is impossible to tell whether the frontal has a sharply demarcated postorbital process and the supposedly sigmoidal ridge on the postorbital process is too weathered to confidently homologize with the structure present in dromaeosaurids). Simply put, this is a damaged and weathered theropod frontal. We consider this taxon to be a nomen dubium.

Utahraptor ostrommaysorum (Kirkland et al., 1993)

Holotype: CEU 184v.400 (CEUM 1430).

Distribution: Barremian, Early Cretaceous, Cedar Mountain Formation, Utah.

ORIGINAL DIAGNOSIS: Following Kirkland et al. (1993), "claws on hand more specialized as cutting blades than in other dromaeosaurs. Lachrymal has distinctly parallel mesial and outer sides, giving it an elongate subrectangular appearance in top view. Premaxilla has base of nasal opening parallel to premaxillary tooth row."

REVISED DIAGNOSIS: A large dromaeosaurid diagnosed by the following combination of characters and autapomorphies: elongate nasal process of premaxilla; quadratojugal L-shaped, without posterior process*; dorsal vertebrae lack pleurocoels; well-developed notch present between lesser trochanter and greater trochanter; distal end of metatarsal III smooth, not ginglymoid.

DISCUSSION: The holotype and hypodigm are based on a single disarticulated, but seemingly associated skeleton from one site (Gaston Quarry) and disarticulated material of multiple individuals from a second site (Dalton Wells) (figs. 42, 43) and even more new material has been collected (J. Choiniere, personal commun.). Additional material pertaining to at least nine individuals is currently under study by Brooks Britt at BYU (Britt et al., 2001) (fig. 43). This material was recovered from Dalton Wells and Yellow Cat Quarries of the Cedar Mountain Formation. In addition to this, material referred to *Nedcolbertia* and two indeterminate coelurosaurs are present in this quarry (Eberth et al., 2006). Based on cervical morphology, one of these taxa may be an ornithomimid (personal obs.: A.H.T.).

Utahraptor is the largest dromaeosaurid known with the largest specimen recovered having a femur length of 565 mm. This individual, however, is only slightly larger than the Mongolian dromaeosaurid *Achillobator giganticus* (femur length = 550 mm). After its initial description, little attention has been paid to the osteology of *Utahraptor*. This may be due to the disarticulated nature of the referred material and the difficulty of referring the isolated elements to a specific taxon given that other theropods are known from the quarry.

Within the hypodigm of *Utahraptor ostrommaysorum*, there is at least one additional small individual (manual phalanx 184v.783/ CEUM 3657), which likely does not pertain to *Utahraptor*. This phalanx cannot be referred to *Utahraptor* nor any other coelurosaur based on apomorphies. Britt et al. (2001) noted that the ungual originally identified as an autapomorphically enlarged manual ungual is in fact the hypertrophied digit II pedal ungual. These authors also noted that the referred surangular may be an unidentifiable bone fragment and that the lacrimal is a *Gastonia* postorbital. We have confirmed the latter two points firsthand. Indeed, the "surangular" is impossible to confidently identify. While it may pertain to a surangular it is also possible that it is a portion of the splenial. As noted by Britt et al. (2001) the quadratojugal (CEU 184v.667/ CEUM 3528) lacks the triradiate shape common to most maniraptorans, given the absence of a distinct quadrate process. The femur of *Utahraptor ostrommaysorum* (e.g., BYU VP15417) bears a well-developed lesser trochanter that, unlike other dromaeosaurids, is separated from the greater trochanter by a distinct notch. As in other dromaeosaurids the parapophyses are distinctly projected on pedicles on the dorsal vertebrae. Unlike other dromaeosaurids, the dorsal vertebrae of *Utahraptor ostrommaysorum* lack pleurocoels.

Britt et al. (2001) proposed that the pubis of *Utahraptor ostrommaysorum* would have been retroverted. They based this inference on the orientation of the pubic peduncle of the ilium. This could not be confirmed based on examination of BYU VP 14389 and we regard the orientation of the pubis as ambiguous for this taxon.

The ischium (BYU VP 10978) referred to *Utahraptor ostrommaysorum* by Britt et al. (2001) is unusual for a dromaeosaurid. The obturator process is very proximally placed compared to most maniraptorans. The ischium lacks the longitudinal ridge that typically divides the dromaeosaurid ischium into an anterior and posterior part (Norell and Makovicky, 1999; Makovicky et al., 2005: char. 168). The shaft of the ischium is also rodlike versus the flat, platelike ischium seen in paravians. In these aspects this ischium is plesiomorphic. Given that multiple coelurosaur taxa are present in at the Dalton Wells site, it seems more likely that this ischium belongs to some other basal coelurosaur (e.g., an ornithomimid) than to *Utahraptor ostrommaysorum*, which would necessitate the presence of an extremely plesiomorphic

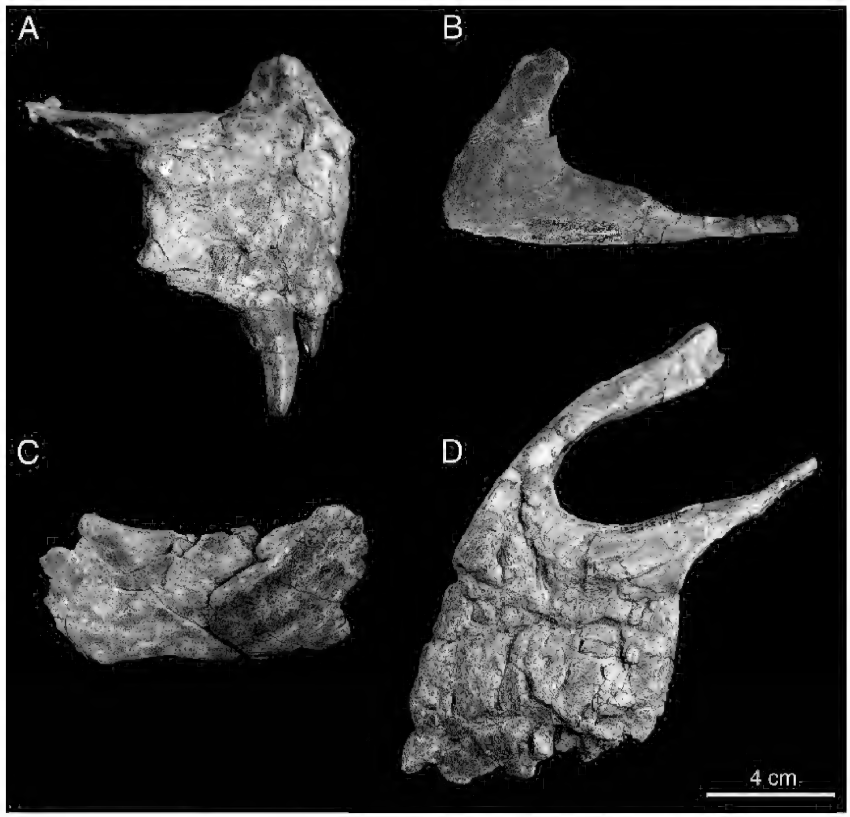


Fig. 42. Select holotype and hypodigm material of *Utahraptor ostrommaysorum*. **A,** right premaxilla (CEUM 1430); **B,** possible right quadratojugal (CEUM 3538); **C,** possible palatine (CEUM 4023); **D,** left premaxilla (CEUM 1370). Note the lack of a distinct posterior process on the quadratojugal.

ischium. The referral of this ischium to the Ornithomimidae is supported by the presence of a distinct semicircular scar on the posterior part of the proximal end of the ischium (present in ornithomimids and tyrannosaurids). Further indirect support for this referral is the presence in the quarry of ornithomimidlike cervical vertebrae (elongate and strongly opisthocoelous) and a postorbital tentatively referred to Ornithomimidae.

Nearly all early iterations of the TWiG matrix found a largely unresolved Dromaeosauridae (Norell et al., 2001; Xu et al., 2002a; Makovicky et al., 2003; Hwang et al., 2002, 2004b; Kirkland et al., 2005; Xu and Norell, 2004). However, more recent versions typically find *Utahraptor* as a derived dromaeosaurids closely related to *Dromaeosaurus albertensis*, *Achillobator giganticus*, and *Adasaurus mongoliensis* (Makovicky et al., 2005; Norell et al., 2006; Turner et al., 2007a, 2007b). Senter (2007) found *Utahraptor* related to a similar set of taxa but specifically found a resolved relationship between *Dromaeosaurus* and *Utahraptor*.

The specimens used in the present analysis all derive from the holotype, hypodigm, and referred material from Dalton Wells and Yellow Cat Quarries (Kirkland et al., 1993; Britt et al., 2001). Given the multitaxon nature of these quarries, specimens that could conceivably be referred to other theropod clades were avoided and codings from these were not included in the matrix.

SOUTH AMERICAN DROMAEOSAURIDS

Austroraptor cabazai Novas et al., 2009

Holotype: MML 195.

Distribution: Campanian-Maastrichtian, Late Cretaceous, Allen Formation, Río Negro

Fig. 43. Referred material of *Utahraptor ostrommaysorum*. **A,** left premaxilla (BYU 7510 14585) in lateral (top) and medial (bottom) views; **B,** right femur (BYU 7510 14281) in lateral view. In **B,** the arrow indicates the notch between the greater and lesser trochanter, which is characteristic of *Utahraptor ostrommaysorum*.

Province, Patagonia, Argentina (fig. 44; table 5).

DIAGNOSIS: A large dromaeosaurid diagnosed by the following combination of characters and autapomorphies (following Novas et al., 2009: 1102–1103): "lacrimal highly pneumatized, with descending process strongly curved rostrally*, and caudal process flaring out horizontally above orbit* (differing from Laurasian dromaeosaurids, but unknown for other unenlagiines); postorbital lacking dorsomedial process for articulation with the frontal*, and with squamosal process extremely reduced (differing from Laurasian dromaeosaurids, but unknown for other unenlagiines); maxillary and dentary teeth small, conical, devoid of serrations and fluted (as in *Buitreraptor*); humerus short, representing slightly less than 50 per cent of femur length (a smaller ratio than in other dromaeosaurids and paravians); pedal phalanx II-2 transversely narrow, contrasting with the extremely robust phalanx IV-2 (differing from other dromaeosaurids, including unenlagiines, but resembling the condition of advanced troodontids)."

DISCUSSION: This taxon is based on disarticulated skeletal remains, which are proposed to represent a single, albeit incompletely preserved, individual (fig. 45). Estimated at nearly 5 m long, *Austroraptor* is one of the largest dromaeosaurid described to date with only *Achillobator* and *Utahraptor* approaching it in size. The phylogenetic analysis conducted by Novas et al. (2009) recovered *Austroraptor* as a derived member of the South American dromaeosaurid clade Unenlagiinae. As support for the placement of *Austroraptor* in Dromaeosauridae, these authors cited the extension of the supratemporal fossa over most of the frontal process of the postorbital, teeth with unconstricted crown-root transition, epipophyses of anterior cervical vertebrae placed distally on the postzygapophyses, and the posterior margin of the cervical centra level with the posterior margin of the neural arch. In the postcranium, *Austroraptor* shares with other unenlagiines dorsal vertebrae with shortened transverse processes, transversely expanded distal ends of the dorsal neural spines, which form a spine table, and a proximally pinched metatarsal III (Novas et al., 2009). Additionally, *Austroraptor* has ventrolateral ridges along the cervical centra as in *Buitreraptor* and *Unenlagia paynemili*.

Novas et al. (2009) noted that *Austroraptor cabazai* differs from other dromaeosaurids and derived paravians in several respects. The humerus is less than half the length of the femur, thus this taxon exhibits relatively short forelimbs. This condition is uncommon in dromaeosaurids (exceptions: *Mahakala omnogovae* and *Tianyuraptor ostromi*) and in particular contrast to the very long forelimbs in the other unenlagiines *Rahonavis ostromi* and *Buitreraptor gonzalezorum*. Additionally, the deltopectoral crest is plesiomorphic relative to other dromaeosaurids, given that it projects anteriorly with a flat lateral face as opposed to the laterally excavated and laterally oriented deltopectoral crest seen in other unenlagiines. The lacrimal has a large excavation containing two foramina in the posterodorsal corner, a condition not known in other dromaeosaur-

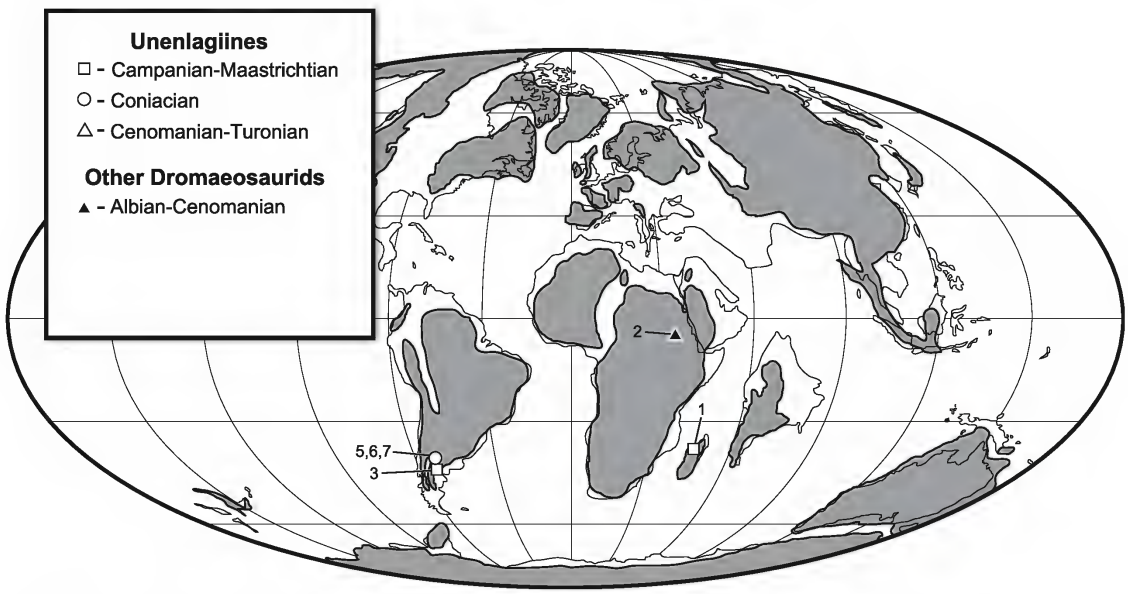


Fig. 44. Geographic distribution of Gondwanan dromaeosaurids illustrated on a paleogeographic globe of the mid-Cretaceous (adapted from Smith et al., 1994).

ids. Novas et al. (2009) also noted that enamel on the tooth surface of *Austroraptor* is fluted in a manner similar to that found in spinosaurid theropods. Not noted by the authors is that the postorbital of *Austroraptor* is bizarre and seemingly very plesiomorphic. All maniraptorans possess a postorbital with a frontal process that curves anterodorsally forming a dorsally concave temporal bar. The postorbital of *Austroraptor* lacks this anterodorsal upturning and in fact has greatly reduced frontal and squamosal processes. The very short squamosal process suggests that either a very long postorbital process on the squamosal was present (a trait that would be dissimilar to most dromaeosaurids) or that there was overall shortening of the temporal region.

Perhaps the most bizarre feature of *Austroraptor* is the strangely disproportionate pedal phalanges (fig. 45D, E, F). Phalanx IV-2 is over twice the width of phalanx II-2.

TABLE 5
Temporal and Geographical Distributions of Gondwanan Dromaeosaurids

	Taxon	Locality	Formation	Age	Reference
1	*Rahonavis ostromi*	Mahajanga Basin, Madagascar	Maevarano Fm.	Campanian-Maastrichtian	Forster et al., 1998
2	Wadi Milk dromaeosaurid	Sudan, Africa	Wadi Milk Fm.	Albian-Cenomanian	Rauhut and Werner, 1995
3	*Austroraptor cabazai*	Patagonia, Argentina	Allen Fm.	Campanian-Maastrichtian	Novas et al., 2009
4	*Buitreraptor gonzalezorum*	Patagonia, Argentina	Candeleros Fm.	Cenomanian-Turonian	Makovicky et al., 2005
5	*Neuquenraptor argentinus*	Patagonia, Argentina	Portezuelo Fm.	Coniacian	Novas and Pol, 2005
6	*Unenlagia comahuensis*	Patagonia, Argentina	Portezuelo Fm.	Coniacian	Novas and Puerta, 1997
7	*Unenlagia paynemili*	Patagonia, Argentina	Portezuelo Fm.	Coniacian	Calvo et al., 2004

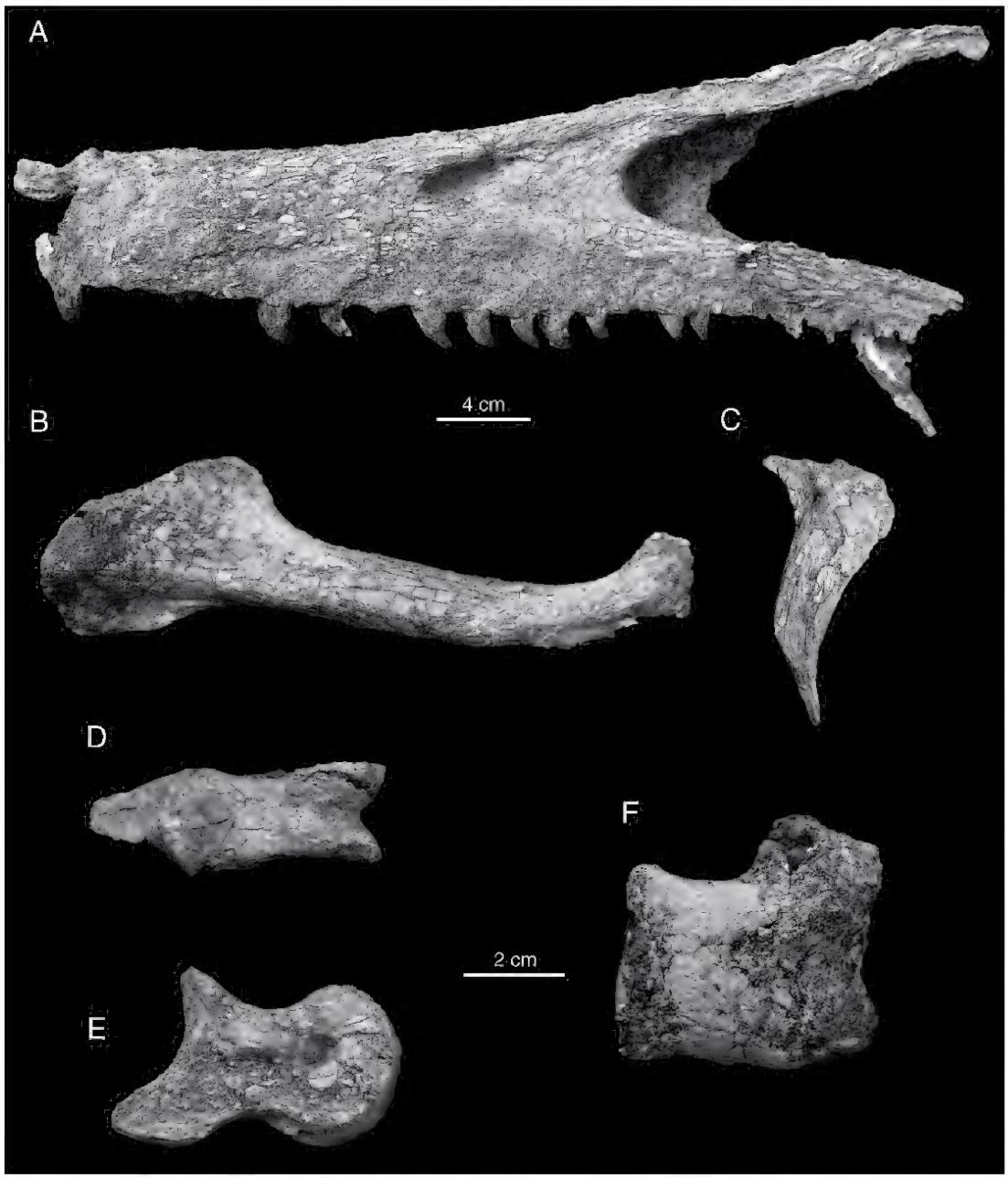


Fig. 45. Select material of *Austroraptor cabazai*. **A,** left maxilla in lateral view; **B,** right humerus in anterodorsal view; **C,** right postorbital in lateral view; **D,** left pedal phalanx II-2 in dorsal view; **E,** left pedal phalanx II-2 in lateral view; **F,** left pedal phalanx IV-2 in dorsal view.

Phalanx II-2 is clearly deinonychosaurian in its morphology; however, phalanx IV-2 is nearly three times the expected width based on similarly sized dromaeosaurids. Contrary to the suggestion of Novas et al. (2009) that a similar condition is present in derived troodontids, taxa such as *Zanabazar mongoliensis* and *Sinornithoides* show very little difference in the width between phalanx II-2 and IV-2. Given the loose association of the holotype material,

the marked size discrepancy in phalangeal elements and plesiomorphic aspect of some of the cranial elements (e.g., postorbital) it is possible that the holotype could be a chimera. However, given that there is not at present any phylogenetic uncertainty (at least within the context of current datasets including *Austroraptor*), as could be expected if the specimen was a chimera, new discoveries will be needed to fully reassess the association of the *Austroraptor* holotype elements.

Buitreraptor gonzalezorum Makovicky et al., 2005

Holotype: MPCA 245 (figs. 46, 47).

Distribution: Cenomanian-Turonian, Late Cretaceous, Candeleros Formation, Río Negro Province, Patagonia, Argentina.

Original Diagnosis: Following Makovicky et al. (2005: 1008) *Buitreraptor* "differs from other theropods in the following unique combination of traits: skull long, exceeding femoral length by 25%; teeth small, unserrated, without root-crown constriction; quadrate with large lateral flange and pneumatic foramen; posterior cervical centra with ventrolateral ridge; furcula pneumatic; brevis shelf expanded and lobate, projects laterally from caudal end of ilium."

Revised Diagnosis: A small dromaeosaurid diagnosed by the following combination of characters and autapomorphies (modified from Makovicky et al., 2005: 1008): skull long, exceeding femoral length by 25%; teeth small, unserrated, without root-crown constriction; quadrate with large lateral flange and pneumatic foramen*; posterior cervical centra with ventrolateral ridge*; furcula pneumatic*; brevis shelf expanded and lobate, projects laterally from caudal end of ilium; differs from other dromaeosaurids by possessing a large maxillary fenestra*; a continuous transition from frontal margin to postorbital process (shared with Troodontidae); dentary bears a deep subalveolar groove (also shared with Troodontidae); flexor process present on humerus.

Discussion: This taxon is based on a nearly complete articulated adult skeleton as well as a partially articulated right hindlimb, sacrum, and pelvis. Found in the Cenomanian-Turonian Candeleros Formation of northwestern Patagonia, *Buitreraptor gonzalezorum* is the oldest dromaeosaurid known from Gondwana. This taxon proved to be a very important discovery because it provided evidence that united previously described Gondwanan dromaeosaurids in a single monophyletic Gondwanan lineage. Makovicky et al. (2005) named this Gondwanan dromaeosaurid lineage Unenlagiinae. This improved phylogenetic context clarified some of the previously problematic morphological data from the incomplete taxa *Unenlagia* and *Neuquenraptor* and led to the suggestion that these two taxa may be synonyms.

The phylogenetic analysis of Makovicky et al. (2005) recovered the purported avialan *Rahonavis ostromi* (from the Late Cretaceous of Madagascar) as a dromaeosaurid included in the Unenlagiinae clade with *Buitreraptor* and *Unenlagia*. *Rahonavis* was previously thought to be a primitive avialan based largely on the long forelimb proportions of the animal, the presence of ulnar papillae (attachment bumps for the follicular ligament of feathers), and features of the ilium. Both the ulnar papillae and ilial characters are known to have wider distributions among paravians (Makovicky et al., 2005; Turner et al., 2007b, 2007c). Furthermore *Buitreraptor* and many basal dromaeosaurids, described subsequent to the discovery of *Rahonavis*, have long forelimb proportions similar to that of *Rahonavis*.

Neuquenraptor argentinus Novas and Pol, 2005

Holotype: MCF PVPH 77 (figs. 48, 49).

Distribution: Coniacian, Late Cretaceous, Portezuelo Formation, Sierra del Portezuelo, Neuquén Province, Argentina.

Diagnosis: Following Novas and Pol (2005: 858), "a probable dromaeosaurid with the following combination of characters: metatarsal II with lateral expansion over the caudal surface of metatarsal III (autapomorphic); metatarsal III proximally pinched; extensor sulcus on proximal half of metatarsus; distal end of metatarsal III is incipiently ginglymoid (to a lesser degree than other dromaeosaurids); pedal digit II with phalanges 1 and 2 subequal in length, and bearing a trenchant ungual phalanx."

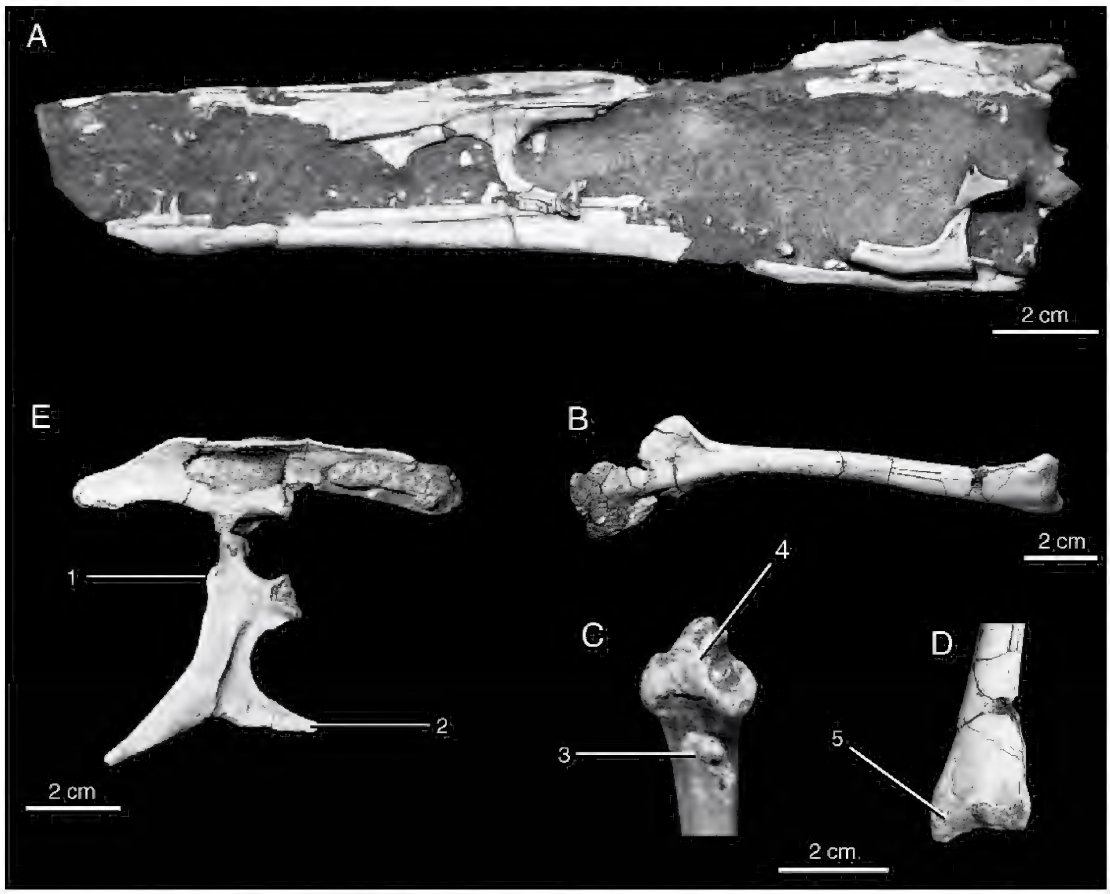


Fig. 46. Select material of *Buitreraptor gonzalezorum* (MPCA 245). **A,** skull in left lateral view; **B,** right humerus in anterodorsal view; **C,** proximal view of left ulna; **D,** dorsal view of distal end of humerus. Important features include: **1,** proximal median process on the posterior edge of the ischium (char. 165.1); **2,** obturator process of ischium located at the distally (char. 169.3) and triangular obturator process with a short base and long anteriorly directed process (char. 234.1); **3,** presence of a small bicipital scar (char. 384.1); **4,** proximal surface of ulna divided into two distinct fossae (char. 144.1); **5,** distal margin of the humerus developed into well-projected flexor process (char. 374.1).

DISCUSSION: This taxon provided important information regarding the presence of dromaeosaurids in South America because of the preservation of unambiguous deinonychosaurian synapomorphies on the pes. The holotype material is fragmentary and incomplete, rendering its exact phylogenetic position within Dromaeosauridae ambiguous.

Neuquenraptor argentinus was distinguished from *Unenlagia* based on differences in femoral proportions; however, both the proximal and distal ends of the femur of *Neuquenraptor* are incomplete. This renders potential statements of proportional differences tenuous. Makovicky et al. (2005) concluded that both femora are nearly identical and are similar in size. Firsthand examination of the femora of both specimens confirms these observations.

Available material referable to *Unenlagia* (Calvo et al., 2004; and see discussions below) is almost identical to *Neuquenraptor* in both size and proportion. Although the cooccurrence and size similarities between the overlapping skeletal elements of *Neuquenraptor* and *Unenlagia* appear to be compelling evidence for possible synonymy as noted by Makovicky et al. (2005), they cautioned for the need for more material to test this hypothesis more rigorously. Additional un-

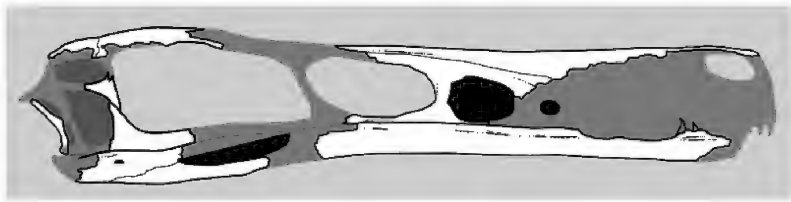


Fig. 47. Interpretive line drawing of the skull of *Buitreraptor gonzalezorum*.

described material of *Neuquenraptor* fails to provide a sufficient amount of new information (personal obs.: A.H.T.). Whereas we think it is likely these two taxa will prove to be synonyms, we feel it prudent to reserve formalizing this until additional overlapping material is found. Makovicky et al. (2005) tentatively treated *Neuquenraptor* as a junior synonym of *Unenlagia* for a secondary phylogenetic analysis. Norell et al. (2006) and Turner et al. (2007a, 2007b) have followed this in subsequent treatments of dromaeosaurid relationship. We follow these authors and previous analyses in continuing to treat these taxa as synonyms for the phylogenetic analysis. Furthermore, phylogenetic sensitivity to *Neuquenraptor*/*Unenlagia* is explored in greater detail in the Discussion.

Unenlagia comahuensis Novas and Puerta, 1997

Holotype: MCF PVPH 78 (figs. 50–52).

Distribution: Turonian-Coniacian, Late Cretaceous, Río Neuquén Formation (now Río Neuquén Subgroup and Portezuelo Formation), Sierra del Portezuelo, Neuquén Province, Argentina.

Original Diagnosis: Following Novas and Puerta (1997: 390), "possesses tall neural spines in posterior dorsals and anterior sacral vertebrae, being nearly twice the height of the centrum; deep lateral pits in the base of the neural spines of these vertebrae; twisted scapular shaft; inflected dorsal margin of postacetabular iliac blade."

Revised Diagnosis: A large dromaeosaurid diagnosed by the following combination of characters and autapomorphies (modified from Novas and Puerta, 1997: 390, incorporating observations from Norell and Makovicky, 1999, and Makovicky et al., 2005): tall neural spines present in posterior dorsals and anterior sacral vertebrae, being nearly twice the height of centrum; deep lateral pits in base of neural spines of posterior dorsal and anterior sacral vertebrae*; twisted scapular shaft; inflected dorsal margin of postacetabular iliac blade; lobate brevis shelf projecting from end of ilium and beyond end of postacetabular lamina; proximodorsal process large, hooked and separated from iliac peduncle of ischium by notch; obturator process with short base and long process extending anteriorly.

Discussion: This taxon is represented by a fragmentary and poorly preserved postcranial skeleton from the Río Neuquén Formation, which has produced other nonavian theropods like the basal alvarezsaurid *Patagonykus puertai*. In the parsimony analysis of Novas and Puerta (1997) *Unenlagia comahuensis* was found as the sister taxon to Avialae.

Unenlagia comahuensis possesses a number of avialanlike features, which lead Novas and Puerta (1997) to regard this taxon as an important transitional nonavian theropod. Norell and Makovicky (1999), however, showed that many of the so-called avialanlike features in *Unenlagia* are also present in dromaeosaurids. These features include the presence of a pubic apron, the posteriorly deflected proximomedial corner of each pubic apron, an expanded cuppedicus fossa on the pubic peduncle (fig. 51), and a laterally oriented glenoid fossa (fig. 50). Furthermore, *Unenlagia comahuensis* preserves a number of dromaeosaurid synapomorphies not present in basal birds; these include stalked parapophyses and a mediolateral expansion of the tip of the neural spine in the posterior dorsal vertebrae (Norell and Makovicky, 1999).

Contrary to earlier analyses that found a sister-group status between Avialae and

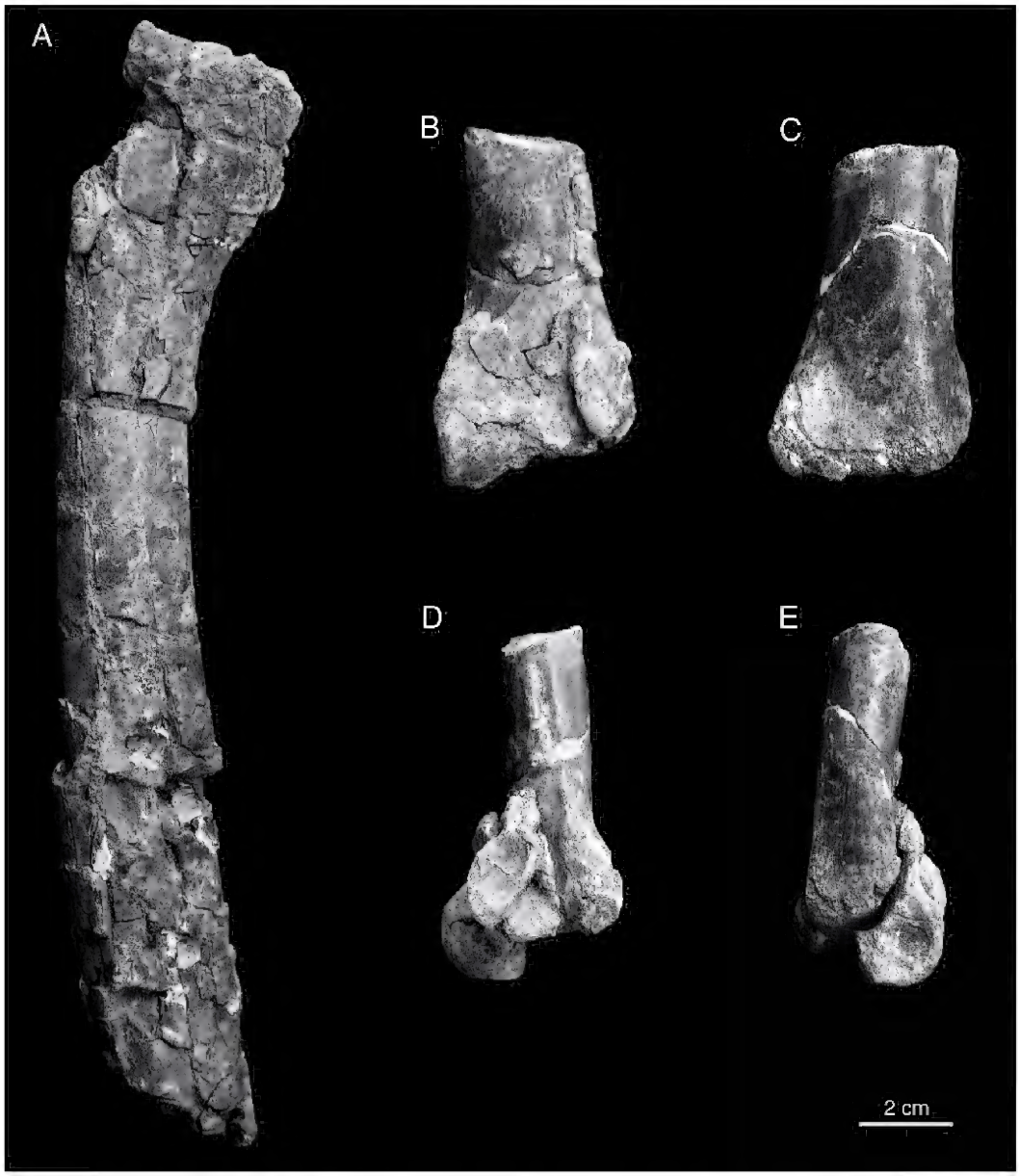


Fig. 48. Select hindlimb material of *Neuquenraptor argentinus* (MCF PVPH 77). **A,** left femur in lateral view; **B,** distal end of left tibiotarsus in anterior view; **C,** distal end of left tibiotarsus in posterior view; **D,** distal end of left tibiotarsus in lateral view; **E,** distal end of left tibiotarsus in medial view.

Unenlagia (Novas and Puerta, 1997; Forster et al., 1998), iterations of the TWiG dataset (Norell et al., 2001; Hwang et al., 2002; Makovicky et al., 2003; Xu and Norell, 2004; Makovicky et al., 2005; Norell et al., 2006; Turner et al., 2007a, 2007b) have consistently found *Unenlagia* nested among other dromaeosaurids. The Unenlagiinae dromaeosaurid clade recovered by Makovicky et al. (2005) including *Unenlagia*, *Rahonavis*, and *Buitreraptor* emerged after the discovery of the much more complete South American *Buitreraptor gonzalezorum* and the associated character analysis of that study. Calvo et al.

(2004) recently described an additional species of *Unenlagia*. For the purposes of our analysis, these two species have been fused into a single *Unenlagia* genus-level terminal taxon.

UNENLAGIA PAYNEMILI CALVO ET AL., 2004

HOLOTYPE: MUCPv-349.

DISTRIBUTION: Turonian–Early Coniacian, Late Cretaceous, Portezuelo Formation, Futalognko site, Neuquén Province, Argentina.

DIAGNOSIS: Following Calvo et al. (2004: 550), "distinguishable from *Unenlagia comahuensis* by possessing more gracile bones, the angle between the anterior rim of the deltopectoral crest and humerus shaft about 116° (opposed to 140° of *Unenlagia comahuensis*) (see fig. 50), a small anterior process on the distal end of pubis, and the distal end of the postacetabular blade of ilium broader and rounded, and a shallower brevis fossa."

DISCUSSION: This taxon is based on a left humerus and left pubis (MUCPv-349) (figs. 53, 54) and referred material including a dorsal vertebra (MUCPv-416), the posterior end of a right ilium (MUCPv-409) (fig. 54), a manual ungual of digit I (MUCPv-343), and pedal phalanx II-1 (MUCPv-415) and phalanx II-2 (MUCPv-1066) (fig. 54).

The new pedal material referred to *Unenlagia* by Calvo et al. (2004) includes pedal phalanges that are almost identical to phalanx II-1 and phalanx II-2 of *Neuquenraptor* in both size and proportions. The phalanx II-2 was not reported in the initial publication and the manual ungual was misidentified as a pedal ungual pertaining to digit I. For the purposes of our analysis the two species of *Unenlagia* have been fused into a single *Unenlagia* taxon.

AFRICAN DROMAEOSAURIDS

RAHONAVIS OSTROMI FORSTER ET AL., 1998

HOLOTYPE: UA 8656 (figs. 55, 56).

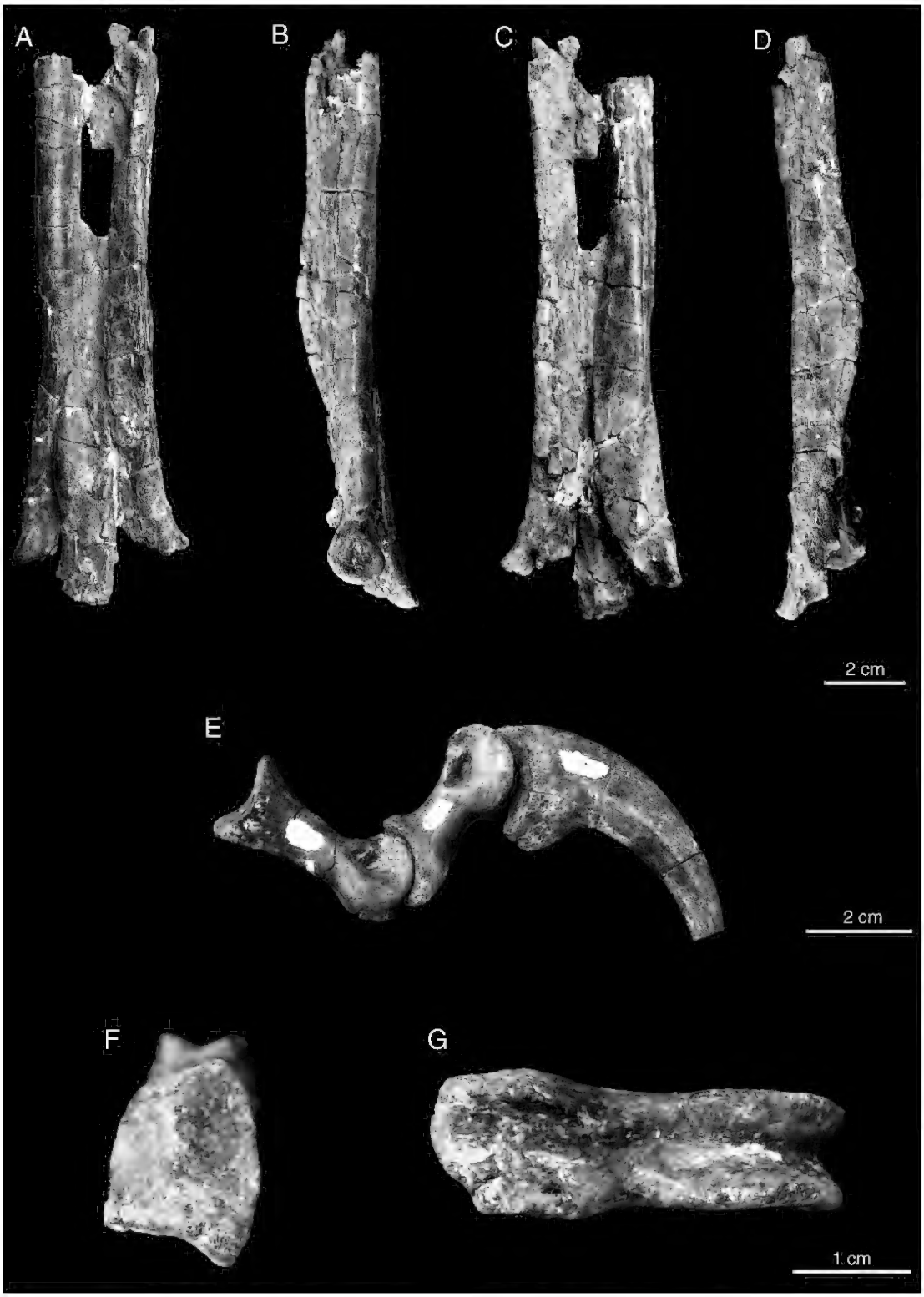
DISTRIBUTION: Maastrichtian, Late Cretaceous, Maevarano Formation, Mahajanga Basin, Madagascar.

ORIGINAL DIAGNOSIS: Following Forster et al. (1998: 1919) "distinguished from all other avians by retention of a robust, hyperextensible, pedal digit II; from all other avians except *Patagonykus* by hyposphene-hypantra articulations on dorsal vertebrae; from *Archaeopteryx* by six fused sacral vertebrae and a greatly reduced fibula lacking contact with the calcaneum; from nonavian theropods, *Archaeopteryx*, and alvarezsaurids by its relatively elongate ulna with ulnar papillae and mobile scapulocoracoid articulation; from all other avians except *Archaeopteryx* and alvarezsaurids by retention of a long tail lacking a pygostyle; and from nonavian theropods by neural canals at least 40% of the height of the dorsal vertebral centra, proximal tibia of equal width and length, lack of a medial fossa on the fibula, and a reversed pedal digit I."

REVISED DIAGNOSIS: A small dromaeosaurid diagnosed by the following combination of characters and autapomorphies: deeply concave glenoid fossa on scapula; elongate acromion process (length greater than length of glenoid)*; long muscle scar above glenoid on lateral face of scapula*; proximally kinked scapular shaft—this is marked by a low tubercle along the dorsal margin of the shaft*; elongate ulna with ulnar papillae; ulnar distal condyle subtriangular in distal view and twisted more than 54° with respect to the proximal end; a neural canal at least 40% of the height of the dorsal vertebral centra; six sacral vertebrae; undivided trochanteric crest, that is distally shifted on the femoral shaft*; prominent and proximally placed fingerlike lateral ridge on femur*; mediolaterally broad cnemial crest with short lateral process*; proximal end of tibia of equal width and length; a greatly reduced fibula lacking contact with the calcaneum; lack of a medial fossa on the fibula.

DISCUSSION: Upon description, *Rahonavis ostromi* (originally "*Rahona,*" but this was amended due to preoccupation by a moth genus) was considered a transitional basal avialan (Forster et al., 1998; Chiappe, 2002). The reason is that, in addition to the new taxon's purported "avian-like" features, it retained the dromaeosaurids feature of an enlarged and hyperextensible claw on digit II, like that seen in dromaeosaurids.

Many of the characters used by Forster et al. (1998) and Chiappe (2002) to support the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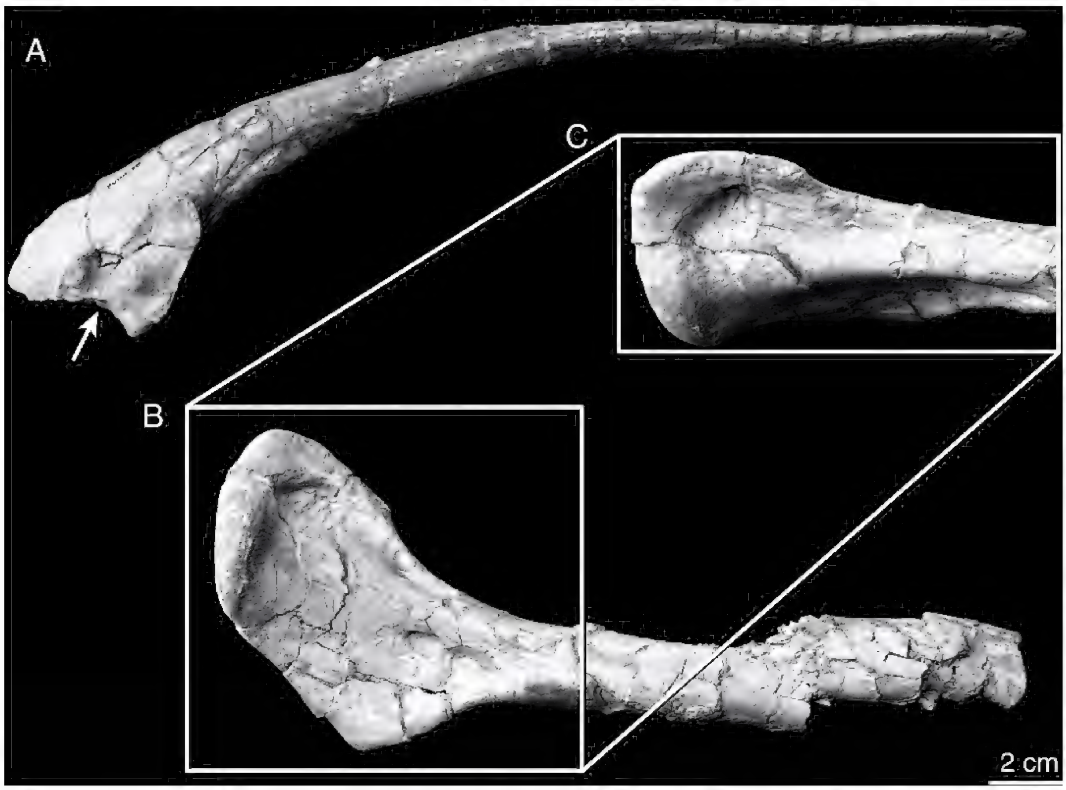

Fig. 50. Select elements of *Unenlagia comahuensis* (MCF PVPH 78). **A,** right scapula in lateral view; **B,** left humerus in anterior view; **C,** close-up of proximal end of humerus in dorsal view. Arrow indicates the laterally oriented glenoid fossa (char. 138.1) characteristic of paravians.

placement of *Rahonavis* within Avialae are now known to have wider distributions. Of the traits proposed by Forster et al. (1998) all are known to have fairly wide occurrences within maniraptorans with the possible exception of the ulnar distal condyle being subtriangular in distal view and twisted more than 54° with respect to the proximal end. The midshaft diameter of the fibula, reduced to 1/5 or less that of the tibia, is also present in dromaeosaurids like *Velociraptor mongoliensis* (IGM 100/986) and many Chinese dromaeosaurids (as well as several troodontids), and the lack of a deep fossa on the medial side of the proximal end of the fibula is common to most derived maniraptorans ranging from oviraptorids (*Citipati osmolskae* IGM 100/978) to dromaeosaurids (*Velociraptor mongoliensis* IGM 100/986) to alvarezsaurids (*Patagonykus puertai* MCF PVPH 37). Four additional characters—preacetabular process of ilium twice as long as postacetabular process, postacetabular process shallow (less than 50% of the depth at the acetabulum) and drawn back into a pointed process, pubic foot only projects

←

Fig. 49. Select pedal elements of *Neuquenraptor argentinus* (MCF PVPH 77). **A,** left metatarsus in anterior view; **B,** left metatarsus in medial view; **C,** left metatarsus in posterior view; **D,** left metatarsus in lateral view; **E,** pedal digit II in medial view; **F,** pedal phalanx II-2 in proximal view; **G,** pedal phalanx II-2 in ventral view.

Fig. 51. Pelvis of *Unenlagia comahuensis* (MCF PVPH 78). **A,** right ilium, pubis, and ischium in lateral view; **B,** medial view of postacetabular blade of right ilium. Important features include: **1,** proximal median process on the posterior edge of the ischium (char. 165.1); **2,** ridge bounding the cuppedicus fossa confluent with the acetabular rim (char. 163.1).

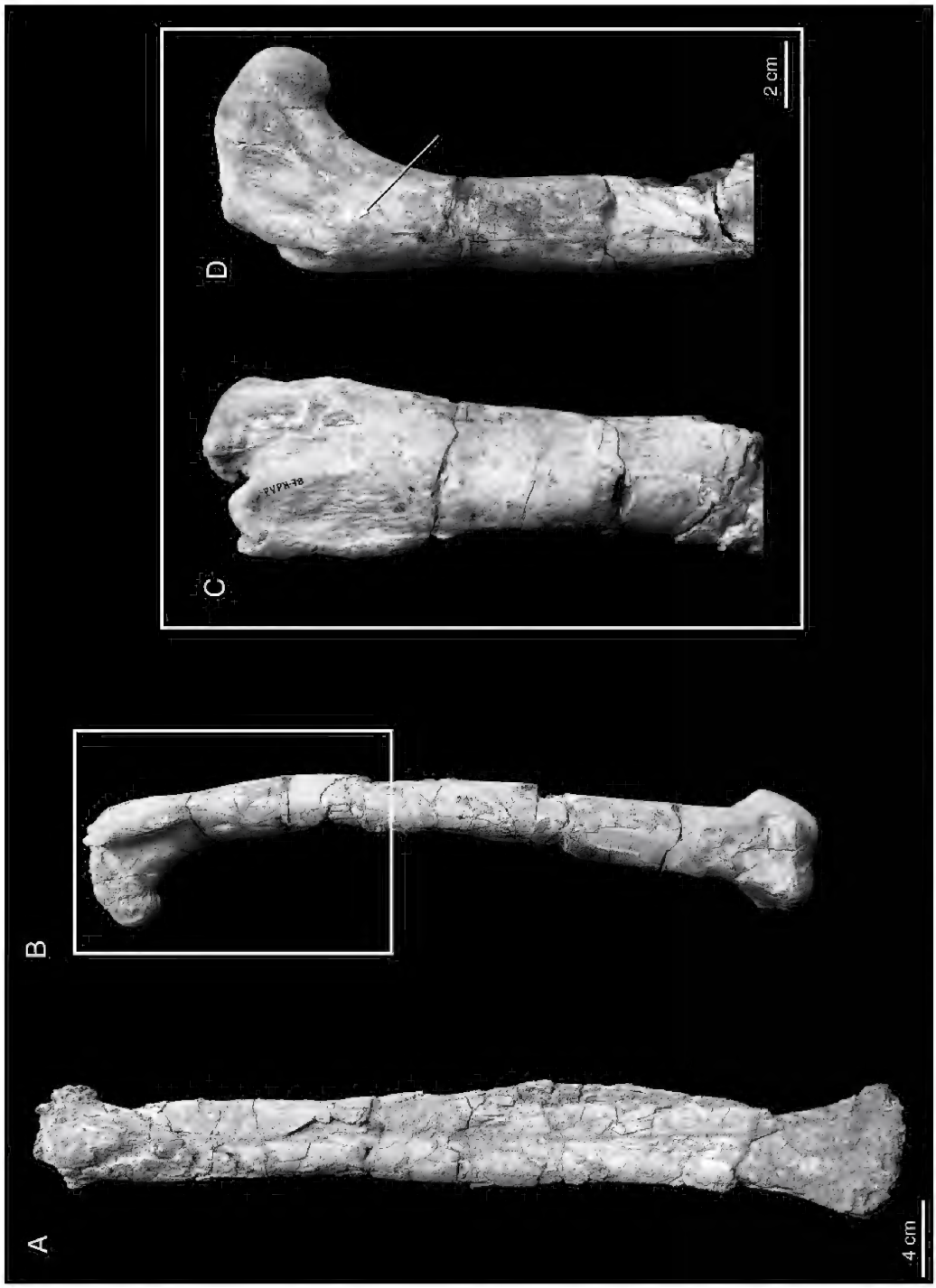

Fig. 52. Select hindlimb elements of *Unenlagia comahuensis* (MCF PVPH 78). **A,** left tibia in anterior view; **B,** left femur in anterior view; **C,** close-up of proximal end of left femur in lateral view; **D,** close-up of proximal end of left femur in posterior view. Arrow indicates the posterior trochanter of the femur.

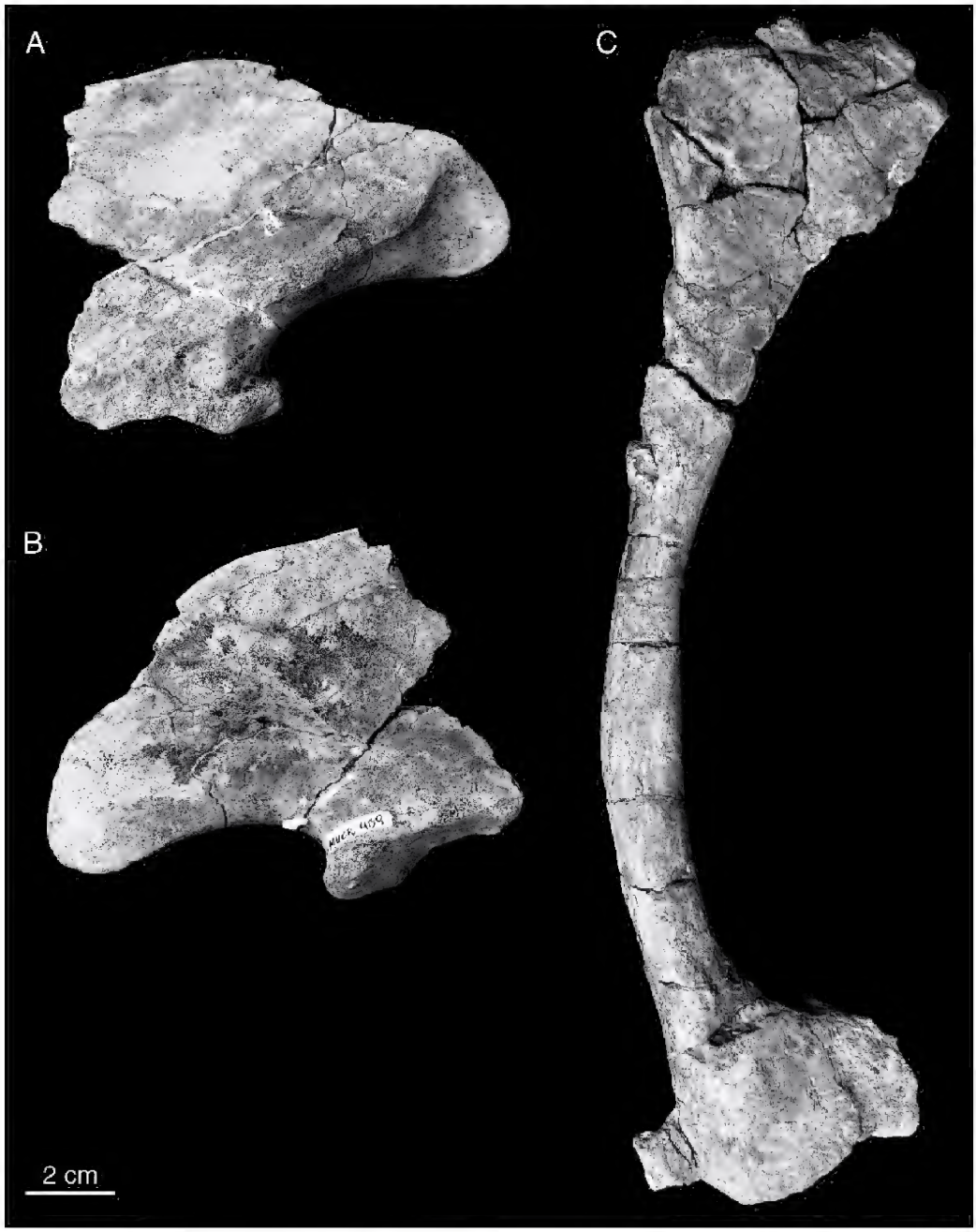

Fig. 53. Select pelvic material of *Unenlagia paynemili*. **A,** right ilium (MUCPv 409) in medial view; **B,** right ilium (MUCPv 409) in lateral view; **C,** right pubis (MUCPv 349) in lateral view.

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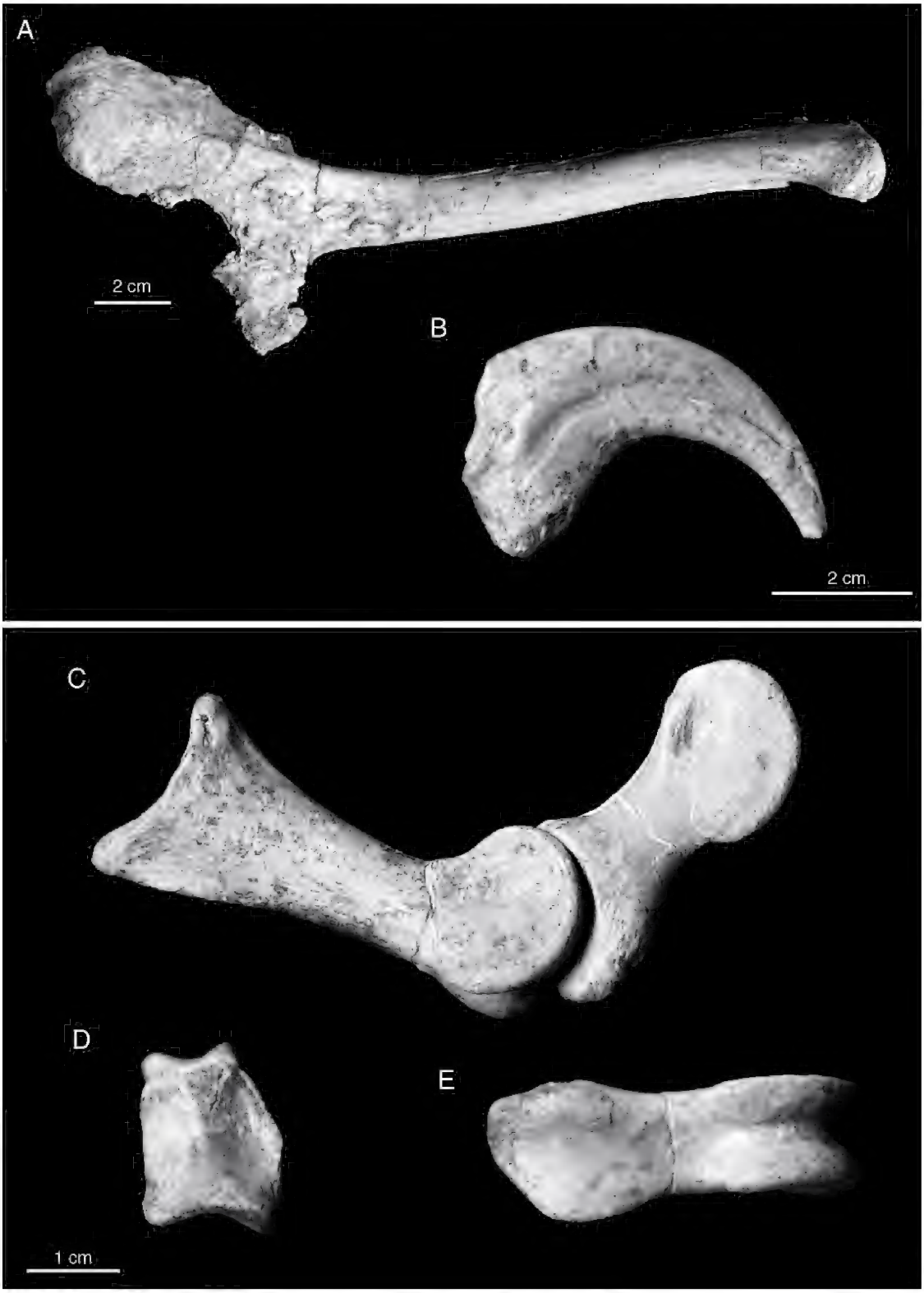
Fig. 54. Select postcranial material of *Unenlagia paynemili*. **A,** left humerus (MUCPv 349) in anterior view; **B,** manual ungual (II?) (MUCPv 343); **C,** pedal phalanx II-1 (MUCPv 415) and phalanx II-2 (MUCPv 1066) in articulation in medial view; **D,** pedal phalanx II-2 (MUCPv 1066) in proximal view; **E,** pedal phalanx II-2 (MUCPv 1066) in ventral view.


A
2 cm
B
2 cm
C
D
E
1 cm

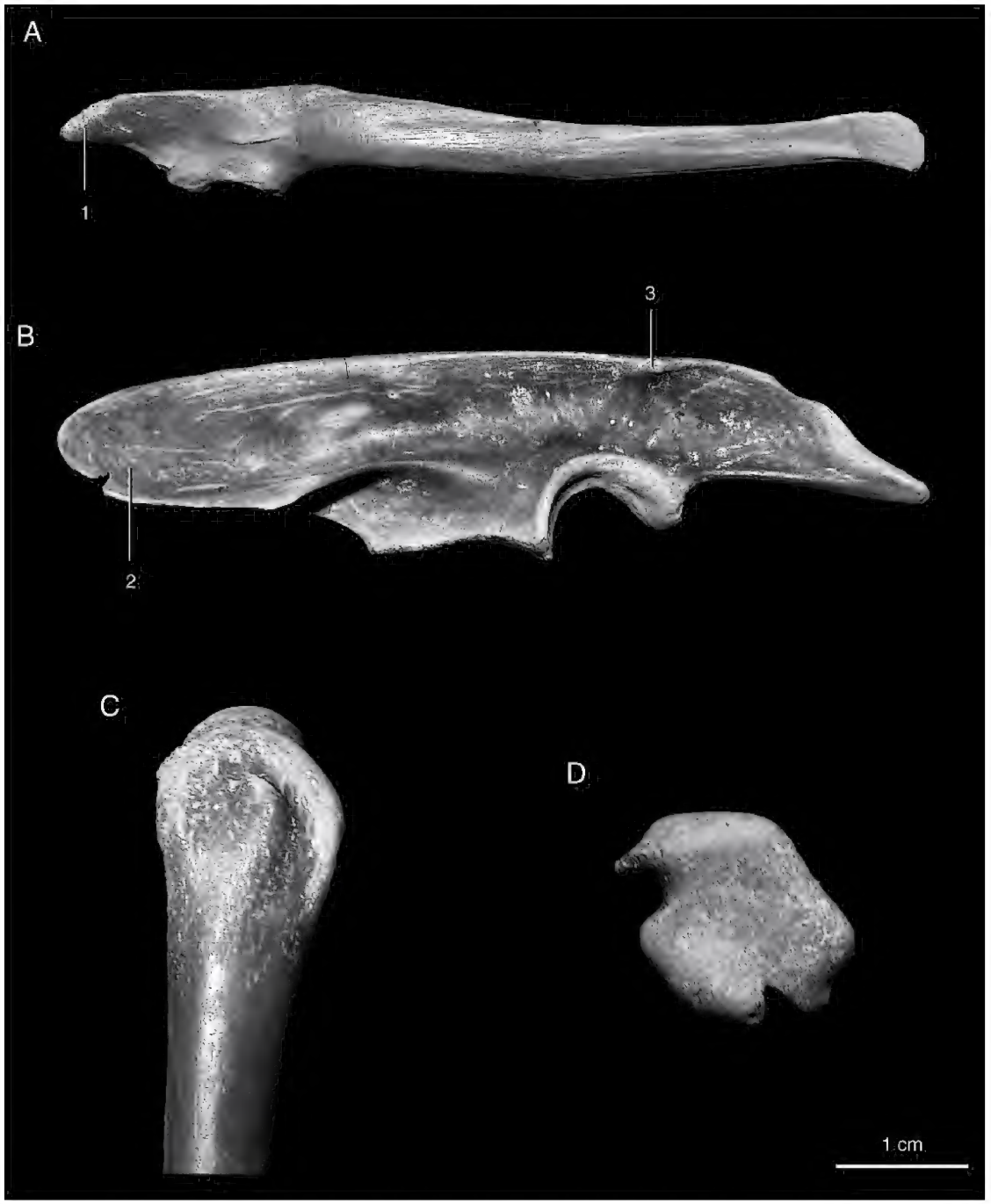


Fig. 55. Select postcranial material of *Rahonavis ostromi* (UA 8656). **A,** left scapula in lateral view; **B,** left ilium in lateral view; **C,** proximal part of right femur in lateral view; **D,** right tibia in proximal view. Important paravian features include: **1,** acromion of scapula laterally everted (char. 133.1) and projecting anteriorly past the articular surface of the coracoid (char. 354.0); **2,** lobate anterior edge of ilium (char. 156.1); **3,** tuber along the dorsal edge of the ilium (char. 160.1).

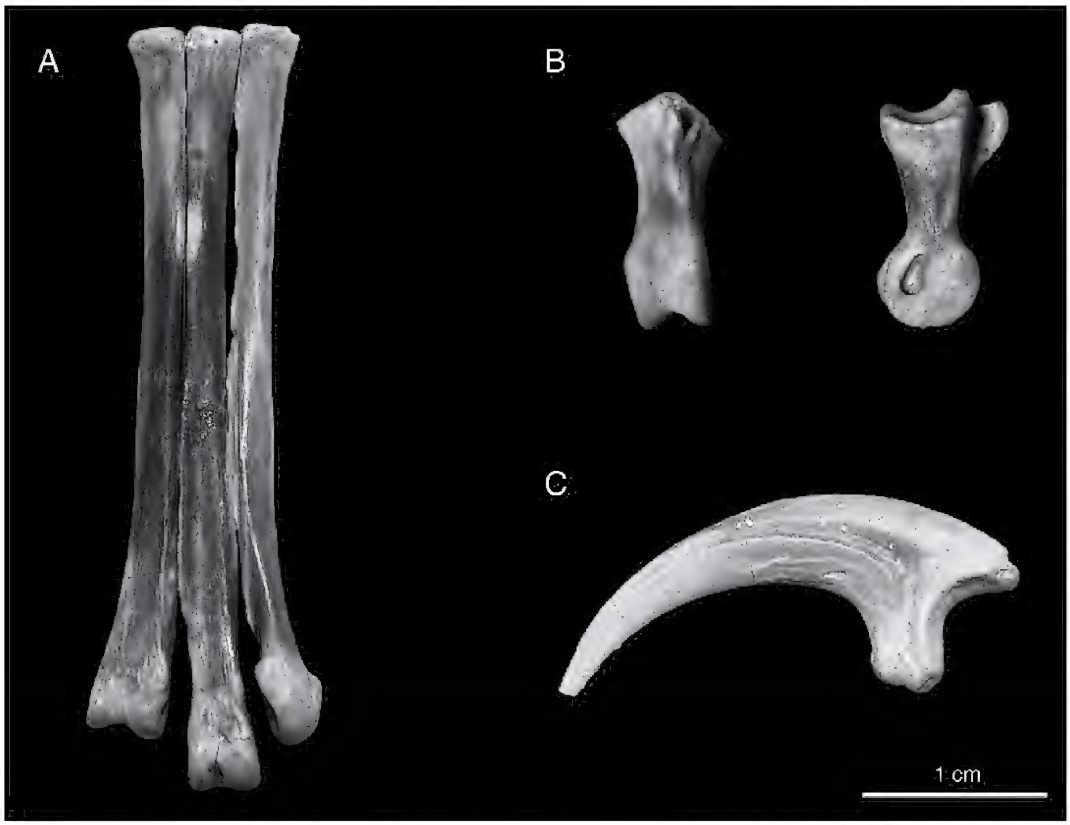


Fig. 56. Select pedal elements of *Rahonavis ostromi* (UA 8656). **A,** left metatarsus in anterior view; **B,** left phalanx II-2 in ventral and lateral views; **C,** ungual phalanx of digit two in lateral view.

caudally, and loss of a femoral neck also show a wide distribution. Although originally identified as possessing a reversed hallux, the morphology of metatarsal I in *Rahonavis ostromi* doesn't differ from other basal paravians with well-represented pedal elements (e.g., *Velociraptor mongoliensis* IGM 100/985, *Archaeopteryx lithographica* [Mayr et al., 2007], *Mei long* IVPP 12733). These taxa do not have fully reversed halluces (also see Middleton, 2002).

Makovicky et al. (2005) recovered *Rahonavis* as a dromaeosaurid related to the other Gondwanan maniraptorans *Unenlagia* and *Buitreraptor*. This analysis incorporated two of the traits Chiappe (2002) proposed uniting *Rahonavis* with birds more derived than *Archaeopteryx*—a fibula that does not reach tarsals and metatarsal II with a tubercle on extensor surface.

Chiappe (2002) proposed that the presence of a well-developed muscle scar for the m. brachialis anticus below the lateral cotyla of the ulna united *Rahonavis* with birds more derived than *Archaeopteryx*. Makovicky et al. (2005) noted that a small depression is present in this region in *Buitreraptor* (MPCA 245) and *Bambiraptor* (AMNH FARB 30556) yet did not include the character in the final analysis. However, the authors did conduct an exploratory analysis with *Rahonavis* and *Confuciusornis* scored as having a developed scar and all other taxa that preserve the ulna scored as lacking it as per Chiappe (2002). That analysis recovered the same set of most parsimonious trees placing *Rahonavis* as a dromaeosaurid.

A ratio of less than 70% between radial and ulnar shaft diameters was also considered diagnostic of *Rahonavis* and pygostylian birds (Chiappe, 2002). Similar ratios are present in *Buitreraptor* (67%; MPCA 245) and other basal deinonychosaurs, such as *Microraptor zhaoianus* (55%–62%; IVPP V13320)

and *Graciliraptor lujiatunensis* (50%; IVPP V13474), suggesting a wider paravian distribution of this trait. Although discussed but not included in the analysis by Makovicky et al. (2005), we have incorporated a character to test the distribution of this morphology.

Rahonavis was reported to have a mobile scapulocoracoid joint, a particularly interesting character because this is generally regarded as a fairly derived avialan morphology occurring somewhere around Ornithothoraces. *Archaeopteryx lithographica* and *Confuciusornis sanctus* have fused nonmobile scapulacoracoid articulations, whereas *Jeholornis* and *Jixiangornis* have incipient ball-and-socket articulation between the scapula and coracoid, but in all three cases the scapula and coracoid are well sutured (albeit not fused) and therefore were probably immobile. If *Rahonavis* does indeed have a mobile scapulocoracoid joint, this distribution of characters in basal avialans strongly suggests separate origins.

Adding to this conclusion is the fact that the supposed mobile scapulocoracoid joint of *Rahonavis* is not morphologically similar to that in ornithothoracines. In those taxa with a true mobile joint, the scapula and coracoid are unfused and the scapula bears a well-developed ball-shaped tubercle that fits into a pit-shaped cotyla on the coracoid. Apparently no such morphology is present in *Rahonavis*, although one cannot comment on the coracoid morphology directly for that taxon because none are known. However, the coracoid facet on the scapula is plesiomorphically flat to very weakly concave in *Rahonavis* and therefore seems unlikely to have enabled mobility of the joint, or at least not in a way that is homologous to that in derived avialans.

The Wadi Milk Dromaeosaurid

This putative dromaeosaurid is known from the Albian-Cenomanian Wadi Milk Formation of northern Sudan (Rauhut and Werner, 1995). The remains of this potential taxon are isolated teeth and a few postcranial elements including a pedal phalanx II-2 and digit II ungual as well as two unguals of uncertain location in the pes. Phalanx II-2 has a deeply grooved distal articular surface and has a modest flexor heel posteriorly as is present in deinonychosaurs. In general appearance it resembles *Pyroraptor olympius*. The flexor process is relatively short compared to most dromaeosaurids and the anterior articular surface is not as highly modified as that seen in either *Velociraptor mongoliensis* or *Deinonychus antirrhopus*. But both the anterior and distal articular surfaces are enlarged and the shaft connecting them is constricted as seen in dromaeosaurids, but not in troodontids. The ungual of the second digit is also enlarged and trenchant as seen in other deinonychosaurs. Based on this information, we agree with Rauhut and Werner's referral of this material to Dromaeosauridae.

Based on tooth morphology, these authors further referred these remains to Velociraptorinae. We disagree with this. The denticles on the teeth are present on both the anterior and posterior carinae and the posterior denticles are much larger than the anterior ones. Although at the time of that publication (Rauhut and Werner, 1995) this morphology may have been unique to Velociraptorinae, this is no longer the case. Denticle size asymmetry is pervasive among dromaeosaurids. Therefore, given this material is insufficient to diagnosis a new taxon, we consider the Wadi Milk material referable to Dromaeosauridae incertae sedis. Nonetheless, this material is important because of its impact on our understanding the geographic distribution of dromaeosaurids, particularly in the light of the recent discoveries of other Gondwanan dromaeosaurids (Novas and Pol, 2005; Makovicky et al., 2005).

ANTARCTIC DROMAEOSAURIDS

The Naze Dromaeosaurid

Case et al. (2007) recently described a potential dromaeosaurid based on two poorly preserved teeth and a partial left pes from the Early Maastrichtian, Camp Lamb Member of the Snow Hill Island Formation. Fragments of metatarsals II, III, and IV were recovered along with phalanx III-1, part of a phalanx from digit IV and part of a distal phalanx from digit III, the posterior half of phalanx II-2, and an distally incomplete digit II ungual. Although, Case et al. (2007) referred this material to Dromaeosauridae, we have reservations. We agree that the digit

II ungual is large and trenchant, but this only allows referral of the material to Deinonychosauria. However, large trenchant claws are also known in therizinosaurs and the stem avialans *Patagonykus* and *Vorona*. The distal articular surface of metatarsal III does appear to be incipiently ginglymoid (a possible dromaeosaurid synapomorphy), but the lack of a ginglymoid articulation on metatarsal II is inconsistent with dromaeosaurid morphology because even the most basal dromaeosaurids have ginglymoid articulations on the distal end of metatarsal II (Turner et al., 2007b). Additionally, it is unclear whether phalanx II-2 has an elongate flexor heel as would be expected for a dromaeosaurid of this size. It is our opinion that this taxon cannot be confidently referred to Dromaeosauridae and should be considered Deinonychosauria incertae sedis.

PART 2: PARAVIAN PHYLOGENY IN THE CONTEXT OF COELUROSAUR EVOLUTION

TAXON SAMPLING

This section is intended to provide a brief outline of the taxonomic sampling scheme employed in this study as well as provide a rationale for such an approach. Further information on the included taxa is listed in appendix 1.

A total of 190 specimens of coelurosaurian theropods were examined firsthand at the collections of 19 different institutions in Argentina, Canada, People's Republic of China, France, Mongolia, the United Kingdom, and the United States. The studied specimens represent a large fraction of known coelurosaur diversity.

The principle analysis in our study includes 109 species-level taxa and two generic-level taxa (*Unenlagia* and *Crax*). The generic-level taxa were scored at this level because in both cases multiple species of each respective genus were used. For *Unenlagia*, this was done to reduce the amount of missing data for it as a terminal taxon, given that *Unenlagia comahuensis* and *Unenlagia paynemili* are both based on largely incomplete species and *Neuquenraptor argentinus* is considered as possibly synonymous with *Unenlagia* (e.g., Makovicky et al., 2005; Turner et al., 2007a, 2007b). The goal of this analysis was to provide the most comprehensive treatment of paravian phylogeny including the largest sample of valid dromaeosaurid, troodontid, and basal avialan taxa available.

Serving at the core of this taxon-sampling regime are 58 coelurosaurian taxa from the Theropod Working Group (TWiG) matrix (Norell et al., 2001). This TWiG matrix served as the base for the datasets of Makovicky et al. (2003), Hwang et al. (2004b), Makovicky et al. (2005), Norell et al. (2006), Turner et al. (2007a), and Turner et al. (2007b), which should be viewed as precursors to and the foundation of the dataset analyzed here. Twenty-two of the avialan taxa in the dataset are derived from the taxon-sampling regime of Clarke et al. (2006).

The coelurosaur outgroup choice was based on previous analyses of the TWiG matrix and confirmed by analyses of basal groups of theropod dinosaurs (Carrano et al., 2002; Rauhut, 2003; Smith et al., 2007). The taxa chosen were the well-known *Allosaurus fragilis* and *Sinraptor dongi*. Since both taxa are equally closely related to Coelurosauria, the better-known and more extensively studied *Allosaurus fragilis* was used to root the trees in this analysis.

Taxon sampling among the basal clades of Coelurosauria closely follows that of the various TWiG iterations (Norell et al., 2001; Hwang et al., 2002; Makovicky et al., 2003; Hwang et al., 2004b; Makovicky et al., 2005; Norell et al., 2006). The largely exhaustive taxon sampling within Ornithomimosauria, Compsognathidae, and Alvarezsauroidea is maintained. Therizinosauria were not heavily sampled and are scored from a few of the best-represented and described taxa—*Segnosaurus galbinensis*, *Alxasaurus elesitaiensis*, and *Erlikosaurus andrewsi*. Oviraptorosauria remains represented basally by *Incisivosaurus gauthieri* and *Caudipteryx zoui*. More derived members of the clade include *Avimimus portentosus*, *Microvenator celer*, *Chirostenotes pergracilis*, *Ingenia yanshani*, *Citipati osmolskae*, *Rinchenia mongoliensis*, *Oviraptor philoceratops*, and *Conchoraptor gracilis*.

Continuing with the additions of Turner et al. (2007a, 2007b) to the basalmost coelurosaurs present in the matrix, putative basal tyrannosauroids in this dataset include *Dilong paradoxus* and *Eotyrannus lengi*. Derived tyrannosaurids are represented by *Tyrannosaurus rex*, *Tarbosaurus bataar*, *Albertosaurus sarcophagus*, *Gorgosaurus libratus*, and *Daspletosaurus torsus*. The two basal tyrannosauroids were studied firsthand for this project while the latter five taxa were based largely on previously published accounts although supplemented at times with reference to available material especially that at the AMNH.

Two other basal coelurosaur taxa of uncertain affinities were added. These are *Coelurus fragilis* (Marsh, 1879) and *Proceratosaurus bradleyi* (von Huene, 1926). Ideas on the phylogenetic position of *Coelurus fragilis* are varied (an issue compounded by its incompleteness), and historically this taxon has been difficult to place within the context of other seemingly closely related forms such as *Ornitholestes hermanni* and *Proceratosaurus bradleyi*. The cladistic analyses that have included *Coelurus fragilis* recover it in a number of different positions basally in Coelurosauria. Rauhut (2003) and Smith et al. (2007) found *Coelurus* as more closely related to compsognathids than to other coelurosaurs, whereas Senter (2007) found *Coelurus* plus *Tanycolagreus topwilsoni* (Carpenter et al., 2005) as the sister group to Tyrannosauroidea. Turner et al. (2007b) found *Coelurus* as more derived than the tyrannosaurids in their analysis (except for *Dilong paradoxus* which was not depicted as being a tyrannosauroid) but basal to all other coelurosaurs. Makovicky and Sues (1998), Zanno et al. (2009), and Zanno (2010a) recovered *Coelurus* as a basal maniraptoran.

Only a few authors have explicitly considered the phylogenetic position of *Proceratosaurus bradleyi*. Holtz (1998) found *Proceratosaurus* to be positioned at the most basal node in the coelurosaur tree. In this analysis, the majority of the terminal taxa examined were supraspecific and therefore provided a weaker test of the position of *Proceratosaurus* than an species-level approach like that taken here. More recently Li et al. (2009), Rauhut et al. (2010), and Brusatte et al. (2010) found this taxon to be a basal tyrannosauroid.

Previous approaches to the phylogenetic relationships of Paraves have had various levels of taxon sampling among the three major constituent clades. The two sampling regimes typically fall into two categories: (1) analyses interested primarily in coelurosaurian relationships and the placement of birds within coelurosaurs (e.g., TWiG iterations); and (2) analyses interested in the interrelationships of birds (Avialae) with only a few nonavialan outgroups (i.e., Clarke, 2004; Clarke et al., 2006; Zhou et al., 2008). Although sufficient for the purposes of those analyses, that level of sampling is insufficient to test for the multiple origins of flight (Mayr et al., 2005), optimization of the *Microraptor*-like four-wing morphology (Xu et al., 2003; Longrich, 2006), or the placement of avialan-like taxa like *Rahonavis ostromi*, *Anchiornis huxleyi*, and new basal taxa with seemingly troodontid and avialan similarities.

Our taxon sampling regime among basal paravians is exhaustive, comprising 52 nonavian paravian taxa (i.e., paravians that do not belong to crown-group Aves). Six crown-group avian taxa were included to help character optimization in this part of the tree by providing accurate codings for characters that affect optimizations near the base of Avialae. This portion of the dataset therefore comprises more than half of the total coelurosaurs sampled for this project. The complete sampling of Dromaeosauridae was discussed at length in Part 1. A brief account of the troodontid and avialan taxa included in the analysis is given below.

TROODONTIDAE: There are currently 15 recognized troodontid species. All but two of these taxa are known from Cretaceous deposits of Asia. *Troodon formosus*, the eponymous taxon for the group, was the first troodontid described (Leidy, 1856) and is known from the Campanian deposits of the Judith River Formation and its stratigraphic equivalents in western North America (Makovicky and Norell, 2004) as well as Maastrichtian units like the Prince Creek Formation of Alaska (Fiorillo, 2008). *Troodon* remains one of the few troodontids represented by multiple individual specimens, although a thorough treatment of these multiple specimens has not been published. Nonetheless, most of the character scorings

for this taxon are based on published descriptions (e.g., Currie and Zhao, 1993) and existing scorings derived from the initial TWiG work (in Norell et al., 2001; Makovicky et al., 2003, etc.). It is worth noting that ongoing work may indicate that all the material considered here as *Troodon formosus* may pertain to more than one species of *Troodon* (e.g., Zanno et al., 2011, in press). Because of the highly nested phylogenetic position of *Troodon formosus*, splitting the *Troodon* terminal into two separate species should have little effect on Troodontidae interrelationships.

Only one specimen of the basal troodontid *Sinovenator changii* (Xu et al., 2002a) has been published, but at least three other specimens exist for this taxon (IVPP uncataloged, and PKU VP 1058). Two specimens exist for *Byronosaurus jaffei* (IGM 100/983 and IGM 100/984; Makovicky et al., 2003). All of these specimens were examined firsthand for this project. All other troodontids species are known from single specimens. *Saurornithoides mongoliensis* (Osborn, 1924b), *Zanabazar junior* (Barsbold, 1974; see Norell et al., 2009), *Sinornithoides mongoliensis* (Russell and Dong, 1993), and *Mei long* (Xu and Norell, 2004) were examined firsthand. The recently described *Xixiasaurus henanensis* was scored based on it published description (Lu et al., 2010). Barsbold et al. (1987) discussed, but did not name, a somewhat plesiomorphic troodontid (IGM 100/44) from the late Albian to early Cenomanian Baruungoyot Svita, Mongolia. This taxon occupies an important position within troodontid phylogeny and is included here based on character scoring from previous iterations of the TWiG matrix.

Five taxa left out of the current project are *Borogovia gracilicrus*, *Urbacodon itemirensis*, *Tochisaurus nemegtensis, Geminiraptor suarezarum*, and *Sinusonasus magnodens*. *Sinusonasus* closely resembles *Sinovenator changii,* but we were not able to examine the holotype firsthand, so did not include it because the illustrations from the description were not sufficient to perform even a conservative scoring of the taxon. The other four taxa, aside from their autapomorphies, preserve character states that are common to all troodontids more derived than *Sinovenator changii*, were unavailable to be examined firsthand, and therefore were not included in the dataset.

The phylogenetic analysis of Turner et al. (2007b) recovered *Jinfengopteryx elegans* (Ji et al., 2005), originally described as an avialan, as a basal troodontid. There are three undescribed troodontids that play an important role in understanding troodontid and paravian phylogeny. One is a Late Jurassic taxon from the Morrison Formation of Wyoming. This taxon is under study by employees of the Wyoming Dinosaur Center and appears to occupy a position near *Sinornithoides* based on the phylogenetic analysis of Hartman et al. (2005). This taxon was not examined and is not included here. Two undescribed troodontids, IGM 100/1126 and IGM 100/1323, were collected from the Late Cretaceous of Mongolia at Ukhaa Tolgod (Hwang et al., 2004a). These taxa are well represented by complete skulls and postcranial material. IGM 100/1323 lacks forelimb material, but IGM 100/1126 preserves most of both hands. The two taxa these specimens represent share numerous characters with troodontids and most closely resemble basal members of the clade such as *Mei* and *Sinovenator*. Nevertheless, a number of putatively avianlike traits have been noted for these taxa (Hwang et al., 2004a). The two specimens were scored for the first time here and included in the phylogenetic analysis. Both of these specimens are currently being described in detail, including through the use of CT data and it is certain that more complete character codings for these taxa will emerge.

AVIALAE: A total of 23 basal avialans and six avians were included in the study. This represents the largest number of basal avialans included in an analysis that considered all of Paraves. This is 27 more avialan taxa than previous versions of the TWiG dataset, 23 more than the analysis of Turner et al. (2007b), and 22 more than the recent analysis by Senter (2007). Generally, these additions follow the taxon sampling regime of Clarke et al. (2006), but with the inclusion of the basal and enigmatic pygostylians *Hongshanornis longicresta* (Zhou and Zhang, 2005) and *Liaoningornis longidigitris* (Hou, 1996), the basal enantiornithine *Pengornis*

houi (Zhou et al., 2008), and the important transitional, long-tailed, basal birds *Jeholornis prima* (Zhou and Zhang, 2002a) and *Jixiangornis orientalis* (Ji et al., 2002b). This taxonomic sampling brings the dataset into close approximation with two other recent analyses of Avialae (You et al., 2006, and Zhou and Zhang, 2006a). We were unable to examine *Gansus yumenensis* and *Ambiortus dementjevi* firsthand so they were not included and therefore our dataset does not match You et al. (2006) completely. Likewise, we were not able to examine *Archaeorhynchus spathula,* so that taxon was not added; our dataset thus does not encompass the entire dataset of Zhou and Zhang (2006a), which otherwise is nearly that of Clarke et al. (2006).

Previous approaches to paravian and avialan phylogenetic relationships were comparatively restricted and did not completely sample the diversity of long-tailed basal avialans. The sampling of basal long-tailed birds here is exhaustive save for *Dalianraptor cuhe* (Gao and Liu, 2005), which has been only briefly described and poorly figured. *Archaeopteryx lithographica* (Meyer, 1861) was included based on the 10 described and available specimens and firsthand examination of the London (BMNH 37001), Eichstätt (JM 2257), Munich (S6), and Thermopolis (WDC-CSG-100) specimens.

Two birds *Jeholornis prima* (Zhou and Zhang, 2002a) and *Shenzhouraptor sinensis* (Ji et al., 2002a) occur in the Early Cretaceous Jiufotang Formation. Described just a few months apart, these two taxa exhibit near identical morphology and have been considered synonymous (Zhou and Zhang, 2006b) and potentially synonymous (Chiappe and Dyke, 2006). We agree with the interpretation of these authors and consider *Shenzhouraptor sinensis* a junior synonym of *Jeholornis prima*. *Jeholornis prima* was scored based on firsthand examination of IVPP V13274, IVPP V13353 and the published descriptions of Zhou and Zhang (2002a, 2003a) and Ji et al. (2002a).

Jixiangornis orientalis (Ji et al., 2002b), from the Yixian Formation, has been included in only one phylogenetic analysis, which found it to be more derived than *Jeholornis*. This taxon was added to the current dataset based on the published description of the holotype plus images of an undescribed CAGS specimen. Contrary to Zhou and Zhang (2006b) *Jixiangornis* is not synonymous with *Jeholornis*. The two taxa are distinguished by a number of differences. For example, *Jeholornis* has six sacral vertebrae and *Jixiangornis* has seven. *Jixiangornis* has uncinate processes whereas no uncinate processes are present in *Jeholornis*. The sternal plates of *Jeholornis* are unfused, but *Jixiangornis* has a single sternal element. *Jeholornis* has a hooked ventral edge to the anterior blade of the ilium whereas *Jixiangornis* does not. *Jeholornis* has a deep ventrally concave cuppedicus fossa, yet *Jixiangornis* lacks a cuppedicus fossa. In *Jeholornis*, the astragalus and calcaneum are unfused to each other and the tibia, whereas there are various degrees of fusion in *Jixiangornis*. *Jeholornis* has gastralia whereas *Jixiangornis* lacks them. These differences are many and significant and definitively support the validity of *Jixiangornis*.

Here, basal short tailed birds are represented by *Confuciusornis sanctus* (Hou et al., 1995a, 1995b; Chiappe et al., 1999) and *Sapeornis chaoyangensis* (Zhou and Zhang, 2002b), which were scored firsthand (five and two specimens respectively). More derived pygostylians such as *Vorona berivotrensis* (Forster et al., 1996), *Neuquenornis volans* (Chiappe and Calvo, 1994), *Gobipteryx minuta* (Elzanowski, 1976; see also Chiappe et al., 2001), *Patagopteryx deferrariisi* (Alvarenga and Bonaparte, 1992), and *Hongshanornis longicresta* (Zhou and Zhang, 2005) were scored firsthand. Whereas the remaining basal pygostylians *Liaoningornis longidigitris*, *Pengornis houi*, *Cathayornis yandica*, and *Concornis lacustris* were scored from published descriptions.

Of the 15 ornithurine taxa included in the analysis, nine were scored based on firsthand examination (*Apsaravis ukhaana* Norell and Clarke, 2001; see also Clarke and Norell, 2002; *Yanornis martini* Zhou and Zhang, 2001; *Yixianornis grabaui* Zhou and Zhang, 2001; *Crypturellus undullatus* Temminck, 1815; *Lithornis*, *Gallus gallus* Linnaeus, 1758; *Crax* Linnaeus, 1758; *Anas platyrhynchus* Linnaeus, 1758; *Chauna torquata* Oken, 1816). Scoring for the remaining taxa (*Songlingornis linghen-*

sis Hou, 1997; *Hesperornis regalis* Marsh, 1880; *Baptornis advenus* Marsh, 1877a; *Ichthyornis dispar* Marsh, 1872; *Iaceornis marshi* Clarke, 2004) was based on published descriptions.

PARAVIAN PROBLEMATICA: Three putative paravian taxa of problematic taxonomic affinity are considered in our study. *Epidendrosaurus ningchengensis*, *Epidexipteryx hui*, and *Pedopenna daohugouensis* are known from the Middle to Late Jurassic Daohugou Formation in Inner Mongolia China. *Epidendrosaurus* has typically been recovered as a basal avialan either just outside (Senter, 2007; Zhang et al., 2008) or just inside (Choiniere et al., 2010) the *Archaeopteryx* node, or in an unresolved position basally in Avialae (Xu and Zhang, 2005) (fig. 4). *Epidexipteryx* was described in a short publication (Zhang et al., 2008) and has been recovered as the sister taxon to *Epidendrosaurus* forming a clade called Scansoriopterygidae (fig. 4B). The phylogenetic position of *Pedopenna* was tested by Xu and Zhang (2005) and found to lie in a polytomy with an unresolved avialan clade and deinonychosaurs. The holotype of *Epidendrosaurus ningchengensis* is an extremely juvenile individual (femur length less than 16 mm long).

A number of similarities exist between *Epidendrosaurus* and *Epidexipteryx*; however, the juvenile nature of *Epidendrosaurus* material makes it difficult to determine whether the differences between these taxa are ontogenetic or taxonomic. Moreover, inclusion of *Epidendrosaurus* in a phylogenetic analysis is problematic because juveniles do not necessarily preserve all the adult morphology needed to accurately place a taxon phylogenetically (Balanoff et al., 2008; Bever and Norell, 2009). Of the three problematic paravian taxa discussed here, we have included the largely complete and nearly full-grown *Epidexipteryx* into the primary phylogenetic analysis. We have chosen not to include *Epidendrosaurus* in the primary analysis but instead explore its potential phylogenetic position in a separate exploratory analysis. Similarly, *Pedopenna* (known from very incomplete remains—a left pes and distal portion of the tibia and fibula) were also included in the exploratory analysis discussed below.

CHARACTER SAMPLING

Previous approaches to paravian systematics have typically been split between nonavialan taxa or strictly avialans, and the character sampling has been drawn along this line as well. Therefore, a significant effort was made in this study to combine these two datasets (primarily the TWiG dataset for nonavialan taxa and Clarke et al., 2006, for avialan taxa). Additional new characters pertinent to basal paravian relationships were added to increase the number of characters relevant to this portion of the tree. This was aided by the study of new Mongolian dromaeosaurids (Norell et al., 2006; Turner et al., 2007a, 2007b), examination of additionally specimens of *Microraptor zhaoianus*, and two undescribed Mongolian troodontids (IGM 100/1323 and IGM 100/1126).

To this end, a compilation of published character sets was made from previous studies (Norell et al., 2001; Hwang et al., 2002; Makovicky et al., 2003; Xu and Norell, 2004; Makovicky et al., 2005; Novas and Pol, 2005; Norell et al., 2006; Turner et al., 2007a, 2007b; Currie and Varricchio, 2004; Currie et al., 2003; Rauhut, 2003; Smith et al., 2007; Nesbitt et al., 2009). These characters were then scrutinized for redundancy, violation of character independence, weak homology statements, arbitrary character-state delimitation (particularly within continuously varying traits), or inconsistency with personal observations. A total of 560 characters were obtained combining new information and published characters. After detailed scrutiny of this character set, a final set of 474 characters remained (appendix 2). Many of the previously used characters were redefined and new character states were incorporated accounting for the additional morphological variation exhibited over the wide range of forms exhibited in the most basal of coelurosaurs (e.g., *Coelurus fragilis*) to the most derived members (e.g., *Gallus gallus*). The character list used here is composed by a fairly even sample of the different anatomical regions (table 6).

CLADISTIC ANALYSIS

Tree Search Strategy

The phylogenetic analysis of paravian theropods within the larger context of Coelurosauria was analyzed with equally weighted parsimony using TNT v. 1.0 (Goloboff et al., 2008a, 2008b). A heuristic tree search strategy was conducted performing 1000 replicates of Wagner trees (using random addition sequences, RAS) followed by TBR branch swapping (holding 10 trees per replicate). The best trees obtained at the end of the replicates were subjected to a final round of TBR branch swapping. Zero-length branches were collapsed if they lacked support under any of the most parsimonious reconstructions (i.e., rule 1 of Coddington and Scharff, 1994). This tree search strategy aims to obtain all the most parsimonious resolutions.

Most Parsimonious Topologies

This search strategy resulted in 1190 most parsimonious trees of 2024 steps (CI = 0.300, RI = 0.740), found in 134 out of the 1000 replications of RAS+TBR. Additional TBR branch swapping of these 1190 trees found 90,970 additional optimal topologies resulting in a total of 92,160 most parsimonious topologies. Due to the desire to sample densely the available paravian taxa, a number of incomplete taxa were included in the analysis. This results in three large zones of tree instability within derived oviraptorosaurs, basal dromaeosaurids, and basal pygostylian avialans. Combined, these zones of instability provide for the extremely large pool of most parsimonious reconstructions.

Tree Summary

Although a very large number of trees were recovered during the tree search, the strict consensus is highly resolved (fig. 57). The largest areas of poor agreement between trees is among basal dromaeosaurids, ornithurine avialans, and to a lesser degree derived oviraptorosaurs and basal coelurosaurs. This lack of resolution in the strict consensus is due to uncertainty in the position of only a few incomplete taxa, most importantly for paravians is the uncertainty of *Pyroraptor olympius* and *Limenavis patagonicus*. When the placement of these taxa are excluded during the strict consensus calculation the resolution markedly improves while still accurately representing the shared topology among all 92,160 fundamental trees (fig. 58). The benefit of this approach as opposed to pruning of these fragmentary taxa from the analysis is that it retains the character optimizations implied by these taxa as well as testing for their relationships among the more completely known coelurosaur taxa.

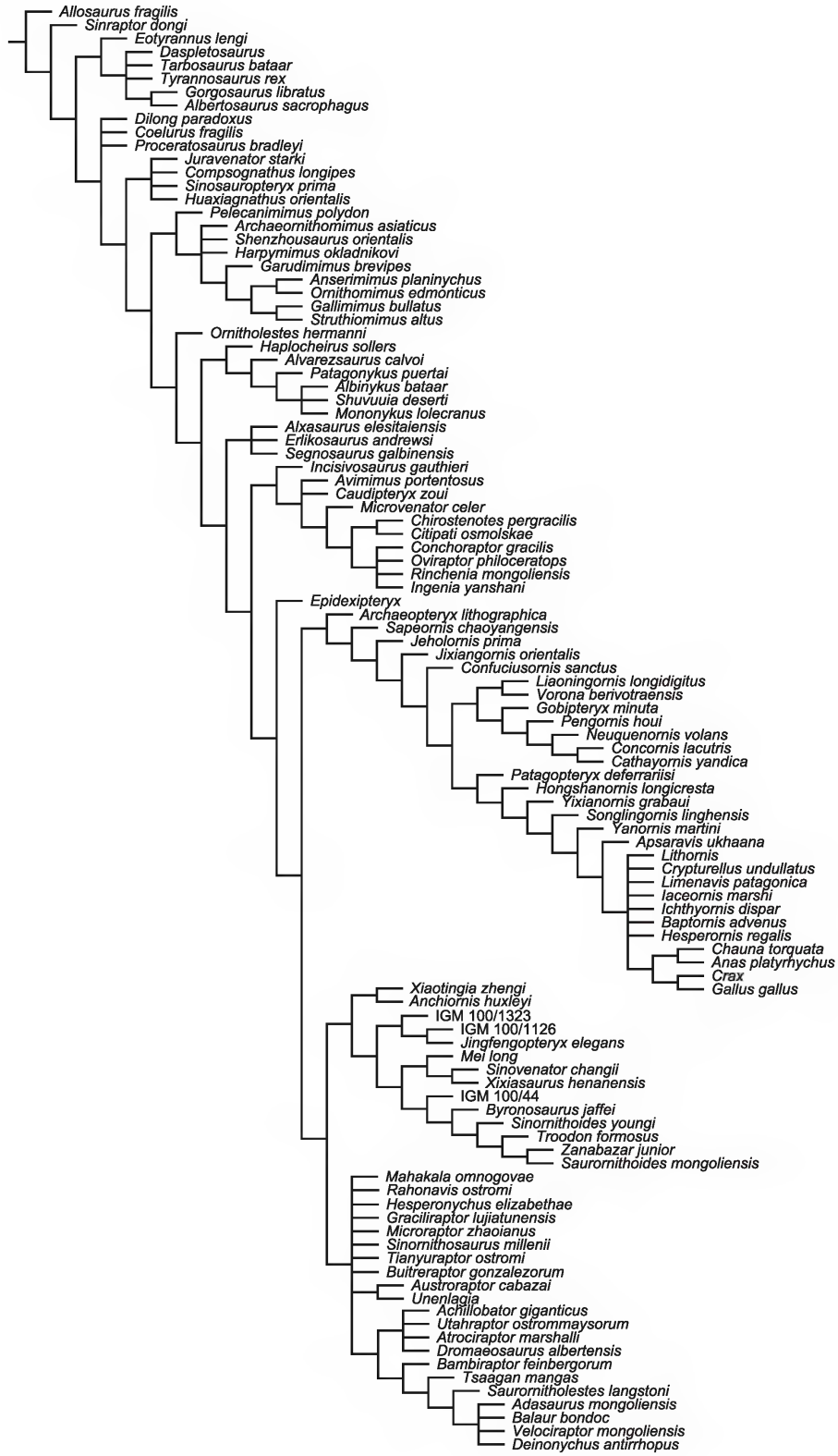
The broad phylogenetic relationships depicted in the consensus tree are congruent with the fundamental topology of previous TWiG analyses (Norell et al., 2001; Hwang et al., 2002; Makovicky et al., 2003; Xu and Norell, 2004; Novas and Pol, 2005; Makovicky et al., 2005; Norell et al., 2006; Turner et al., 2007a, 2007b). This is the case even though total character sampling and taxon sampling was nearly doubled. The monophyly of the major clades of Coelurosauria were recovered including Dromaeosauridae, Troodontidae, Avialae, Oviraptorosauria, Therizinosauria, Alvarezsauroidea, Compsognathidae, Ornithomimosauria, and Tyrannosauroidea.

TABLE 6
Character Breakdown by Anatomical Region

Anatomical Region	Number of Characters	Percentage
Skull	166	35%
Dental	16	3%
Integument	3	<1%
Vertebral Column	54	11%
Forelimb	121	26%
Hindlimb	112	24%

→

Fig. 57. Strict consensus topology of 92,160 most parsimonious reconstructions of coelurosaurian relationships found in the phylogenetic analysis of 474 characters and 111 taxa. Tree length equals 2024 steps; CI = 0.300; RI = 0.740.


Allosaurus fragilis
Sinraptor dongi
Eotyrannus lengi
Daspletosaurus
Tarbosaurus bataar
Tyrannosaurus rex
Gorgosaurus libratus
Albertosaurus sacrophagus
Dilong paradoxus
Coelurus fragilis
Proceratosaurus bradleyi
Juravenator starki
Compsognathus longipes
Sinosauropteryx prima
Huaxiagnathus orientalis
Pelecanimimus polydon
Archaeornithomimus asiaticus
Shenzhousaurus orientalis
Harpymimus okladnikovi
Garudimimus brevipes
Anserimimus planinychus
Ornithomimus edmonticus
Gallimimus bullatus
Struthiomimus altus
Ornitholestes hermanni
Haplocheirus sollers
Alvarezsaurus calvoi
Patagonykus puertai
Albinykus bataar
Shuvuuia deserti
Mononykus olecranus
Alxasaurus elesitaiensis
Erlikosaurus andrewsi
Segnosaurus galbinensis
Incisivosaurus gauthieri
Avimimus portentosus
Caudipteryx zoui
Microvenator celer
Chirostenotes pergracilis
Citipati osmolskae
Conchoraptor gracilis
Oviraptor philoceratops
Rinchenia mongoliensis
Ingenia yanshani
Epidexipteryx
Archaeopteryx lithographica
Sapeornis chaoyangensis
Jeholornis prima
Jixiangornis orientalis
Confuciusornis sanctus
Liaoningornis longidigitus
Vorona berivotraensis
Gobipteryx minuta
Pengornis houi
Neuquenornis volans
Concornis lacutris
Cathayornis yandica
Patagopteryx deferrariisi
Hongshanornis longicresta
Yixianornis grabaui
Songlingornis linghensis
Yanornis martini
Apsaravis ukhaana
Lithornis
Crypturellus undullatus
Limenavis patagonica
Iaceornis marshi
Ichthyornis dispar
Baptornis advenus
Hesperornis regalis
Chauna torquata
Anas platyrhychus
Crax
Gallus gallus
Xiaotingia zhengi
Anchiornis huxleyi
IGM 100/1323
IGM 100/1126
Jingfengopteryx elegans
Mei long
Sinovenator changii
Xixiasaurus henanensis
IGM 100/44
Byronosaurus jaffei
Sinornithoides youngi
Troodon formosus
Zanabazar junior
Saurornithoides mongoliensis
Mahakala omnogovae
Rahonavis ostromi
Hesperonychus elizabethae
Graciliraptor lujiatunensis
Microraptor zhaoianus
Sinornithosaurus millenii
Tianyuraptor ostromi
Buitreraptor gonzalezorum
Austroraptor cabazai
Unenlagia
Achillobator giganticus
Utahraptor ostrommaysorum
Atrociraptor marshalli
Dromaeosaurus albertensis
Bambiraptor feinbergorum
Tsaagan mangas
Saurornitholestes langstoni
Adasaurus mongoliensis
Balaur bondoc
Velociraptor mongoliensis
Deinonychus antirrhopus

Allosaurus fragilis
Sinraptor dongi
Eotyrannus lengi
Daspletosaurus
Tarbosaurus bataar
Tyrannosaurus rex
Gorgosaurus libratus
Albertosaurus sacrophagus
Dilong paradoxus
Coelurus fragilis
Proceratosaurus bradleyi
Juravenator starki
Compsognathus longipes
Sinosauropteryx prima
Huaxiagnathus orientalis
Pelecanimimus polydon
Archaeornithomimus asiaticus
Shenzhousaurus orientalis
Harpymimus okladnikovi
Garudimimus brevipes
Anserimimus planinychus
Ornithomimus edmonticus
Gallimimus bullatus
Struthiomimus altus
Ornitholestes hermanni
Haplocheirus sollers
Alvarezsaurus calvoi
Patagonykus puertai
Albinykus bataar
Shuvuuia deserti
Mononykus olecranus
Alxasaurus elesitaiensis
Erlikosaurus andrewsi
Segnosaurus galbinensis
Incisivosaurus gauthieri
Avimimus portentosus
Caudipteryx zoui
Microvenator celer
Chirostenotes pergracilis
Citipati osmolskae
Conchoraptor gracilis
Oviraptor philoceratops
Rinchenia mongoliensis
Ingenia yanshani
Epidexipteryx
Archaeopteryx lithographica
Sapeornis chaoyangensis
Jeholornis prima
Jixiangornis orientalis
Confuciusornis sanctus
Liaoningornis longidigitus
Vorona berivotraensis
Gobipteryx minuta
Pengornis houi
Neuquenornis volans
Concornis lacutris
Cathayornis yandica
Patagopteryx deferrariisi
Hongshanornis longicresta
Yixianornis grabaui
Songlingornis linghensis
Yanornis martini
Apsaravis ukhaana
Iaceornis marshi
Ichthyornis dispar
Hesperornis regalis
Baptornis advenus
Crypturellus undullatus
Lithornis
Chauna torquata
Anas platyrhychus
Crax
Gallus gallus
Xiaotingia zhengi
Anchiornis huxleyi
IGM 100/1323
IGM 100/1126
Jingfengopteryx elegans
Mei long
Sinovenator changii
Xixiasaurus henanensis
IGM 100/44
Byronosaurus jaffei
Sinornithoides youngi
Troodon formosus
Zanabazar junior
Saurornithoides mongoliensis
Mahakala omnogovae
Rahonavis ostromi
Buitreraptor gonzalezorum
Austroraptor cabazai
Unenlagia
Shanag ashile
Hesperonychus elizabethae
Graciliraptor lujiatunensis
Microraptor zhaoianus
Sinornithosaurus millenii
Tianyuraptor ostromi
Achillobator giganticus
Utahraptor ostrommaysorum
Atrociraptor marshalli
Dromaeosaurus albertensis
Bambiraptor feinbergorum
Tsaagan mangas
Saurornitholestes langstoni
Adasaurus mongoliensis
Balaur bondoc
Velociraptor mongoliensis
Deinonychus antirrhopus

Relationships of note are the sister-group status of Dromaeosauridae and Troodontidae (constituting the Deinonychosauria), which together with Avialae constitute Paraves.

Important conclusions include: *Pyroraptor olympius* never falls within the derived Laurasian dromaeosaurid clade; *Shanag ashile* is more derived than unenlagiines but outside of microraptorines; Unenlagiinae is monophyletic with *Rahonavis* the most basal member; interrelationships of Microraptorinae are unresolved and *Tianyuraptor* nests within the clade; a monophyletic Laurasian clade comprised of a monophyletic Velociraptorinae and Dromaeosaurinae is present; *Rahonavis ostromi* is a dromaeosaurid and placing it into Avialae is markedly unparsimonious; *Bambiraptor feinbergorum* nests with velociraptorines and is not closely related to Chinese microraptorines; a new clade of basal Troodontidae is discovered consisting of *Jinfengopteryx elegans* and two undescribed Mongolian troodontids IGM 100/1323 and IGM 100/1126; *Xiaotingia zhengi* and *Anchiornis huxleyi* are sister taxa at the base of Troodontidae; *Sapeornis chaoyangensis* is more basal within Avialae than both *Jeholornis prima* and *Jixiangornis orientalis,* in spite of the presence of a pygostyle, and therefore is the only known nonpygostylian avialan with a pygostyle.

Areas of Uncertainty

Four regions of coelurosaur phylogeny exhibited disagreement among the fundamental trees and resulted in topological uncertainty in our strict consensus. These areas are basal coelurosaurs, derived oviraptorosaurs, basal dromaeosaurids, and ornithurine avialans. The character matrix employed in this study was not constructed with resolution of all these parts of the tree (except basal dromaeosaurids) in mind. Furthermore, phylogenetic resolution of basal coelurosaurs, derived oviraptorosaurs, and therizinosaurs are the subject of ongoing research with datasets constructed specifically to elucidate these relationships (Zanno, 2010a; Balanoff, 2011; Choiniere et al., 2010). Therefore, only two of these areas of uncertainty will be discussed further: basal dromaeosaurids and ornithurine avialans.

Basal Dromaeosauridae

In the strict consensus, the relationships among dromaeosaurids more basal than the Laurasian Velociraptorinae + Dromaeosaurinae clade are completely unresolved. This is due to the highly variable position of *Pyroraptor olympius*. *Pyroraptor olympius* is known from a few pedal phalanges, a metatarsal II, a radius and ulna, and a vertebra (Allain and Taquet, 2000). Examination of the fundamental trees shows that *Pyroraptor olympius* can occupy at least 23 alternate positions (fig. 59). Only one of these positions, however, is supported by unambiguous character data. *Pyroraptor olympius* shares with all dromaeosaurids the development of a ginglymoid distal end on metatarsal II (char. 201.1). This is a quintessential dromaeosaurid synapomorphy first noted by Ostrom (1969a) in *Deinonychus antirrhopus* and appears to relate to a reduction in medial and lateral excursion of the hypertrophied digit II in dromaeosaurids. The lability of this incomplete taxon is currently due to the absence of data and not character conflict. This is evinced by the fact that deletion of *Pyroraptor* from the analysis does not result in shorter trees.

Ornithurine Avialans

In the strict consensus, all non-neognath ornithurines form a polytomy. When the alternate positions of *Limenavis patagonicus*

←

Fig. 58. Reduced strict consensus topology of the same 92,160 most parsimonious reconstructions. *Pyroraptor olympius* and *Limenavis patagonicus* have been excluded from the consensus.

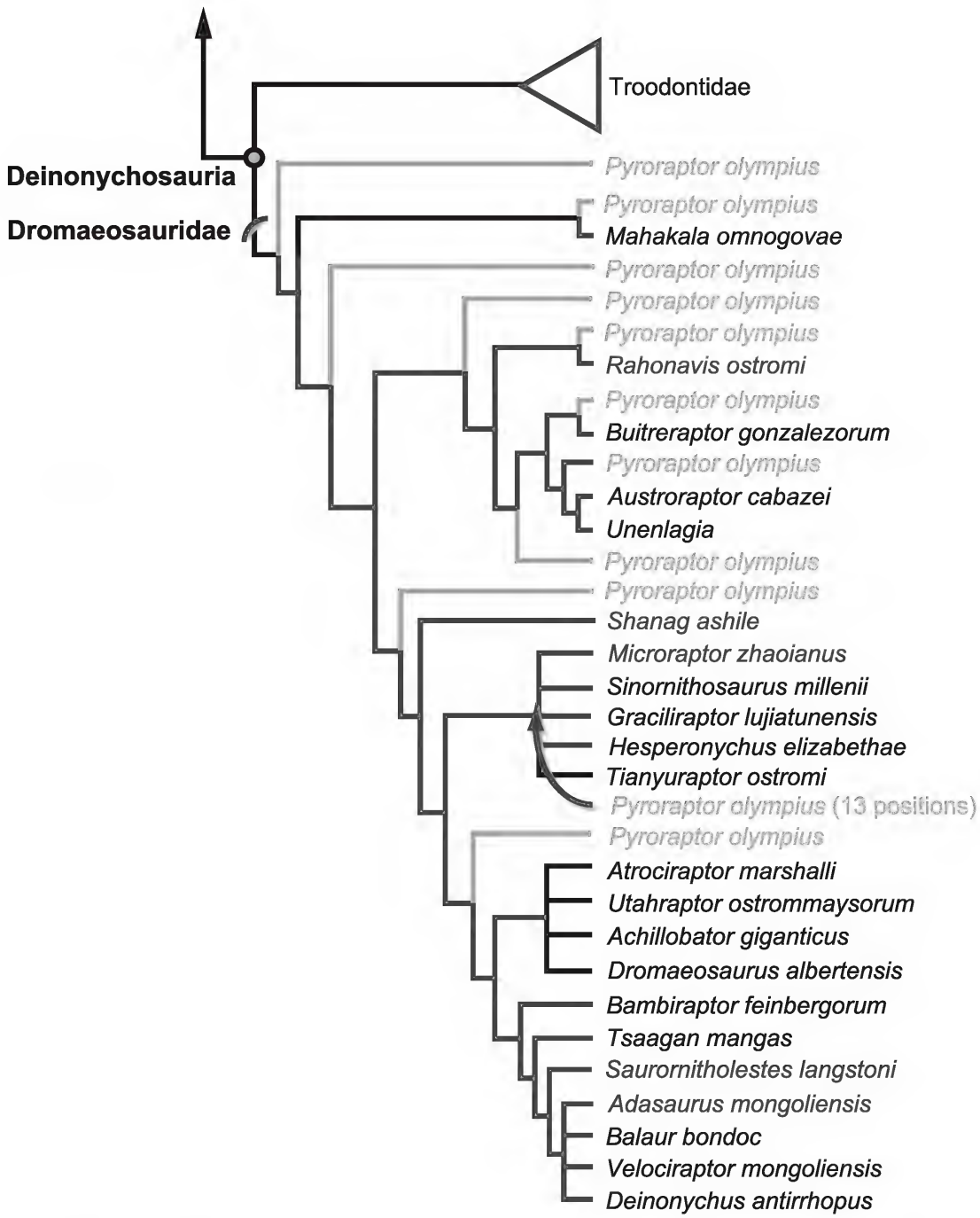


Fig. 59. Cladogram summarizing the 23 alternate positions that *Pyroraptor olympius* can take among dromaeosaurids.

are ignored, the resolution of non-neognath ornithurines greatly improves. *Limenavis* can occupy eight locations among ornithurines (fig. 60); however, only one of these is supported by an unambiguous synapomorphy. *Limenavis* groups with Ornithurae (*Hesperornis* + Aves) based on a slightly raised bicipital scar on the ulna (char. 421.1).

Tree Description

The main point of interest for this analysis is paravian relationships, so that is the portion of the phylogeny that will be described in the most detail. Nonetheless, the characters supporting the major coelurosaurian clades along the spine of the tree leading to Paraves will be discussed here. We will begin at the base of the tree moving crownward. A complete list of synapomorphies can be found in appendix 4.

As discussed above, the consensus topology depicting the interrelationships of Coelurosauria is well resolved when two poorly known/highly incomplete taxa are ignored (*Pyroraptor olympius* and *Limenavis patagonicus*). This reduced strict consensus (fig. 58) forms the basis for the discussion to follow. For each clade discussed below, if formally named, the definition is given prior to the discussion of synapomorphies for this clade. Unless specifically noted, these definitions follow the author(s) that named the clade. Additionally, character numbers are cited for each of the diagnostic characters. The numbering of these characters corresponds to the list of used characters included in appendix 2. In this description, character numbers are followed by a period then the synapomorphic character state number.

Coelurosauria Huene, 1914

Definition: A stem-based monophyletic group containing *Passer domesticus* (Linnaeus, 1758) and all theropods closer to it than to *Allosaurus fragilis* Marsh, 1877b (sensu Holtz, 1994).

Coelurosauria is an extremely well-supported group with eight unambiguous synapomorphies and very strong nodal support (see below) (figs. 61, 66). All coelurosaurs are united by the presence of a number of derived features of the skull, vertebral column, and hindlimb. In the skull, they are characterized by extensive palatal shelves on the maxilla that form a long secondary palate (char. 25.1). This feature becomes particularly well developed in some paravian taxa like troodontids (e.g., *Byronosaurus jaffei* Makovicky et al., 2003). This is a completely nonhomoplastic character that has remained a consistent synapomorphy for Coelurosauria across multiple datasets and a number of iterations of the TWiG dataset (Sereno, 1999; Norell et al., 2001; Makovicky et al., 2003; Hwang et al., 2004b; Turner et al., 2007a).

The quadratojugals of coelurosaurs are typically a reversed L shape, as they lack a horizontal process posterior to the ascending process (char. 35.0), although reversals to the plesiomorphic condition are spread across various clades. *Ornitholestes hermanni*, *Erlikosaurus andrewsi*, *Caudipteryx zoui* show reversals to the Y-shaped quadratojugal and a reversal supports Dromaeosauridae monophyly, although the trait is not known in the basal *Mahakala omnogovae*. A reduced prefrontal ossification is optimized as ancestral for coelurosaurs (char. 40.1). Originally considered by Gauthier (1986) as a synapomorphy for Maniraptora, this optimization is based on the presence of a reduced prefrontal in the basally placed Tyrannosauroidea and *Dilong paradoxus*, which exhibit reduced prefrontal ossifications. The character witnesses notable reversals in ornithomimosaurs, *Sinosauropteryx prima*, *Shuvuuia deserti*, *Sinornithosaurus millenii, Deinonychus antirrhopus*, and possibly *Erlikosaurus*. Also near the posterior margin of the snout, the frontals narrow anteriorly as a wedge between the nasals (char. 41.0), this character reverses to the transverse frontal/nasal suture at the clade including Alvarezsauroidea + Therizinosauria + Oviraptorosauria + Paraves.

Also ancestral for coelurosaurs are the so-called D-shaped premaxillary teeth (char. 91.1). This is better defined as asymmetrical tooth crowns, because of their rounded, labial-sided, and flat lingual surface. This optimization is common to previous TWiG matrices (Norell et al., 2001, Hwang et al., 2004b; Makovicky et al., 2005; Turner et al., 2007a) and is due to occurrence of this morphology among basal members of

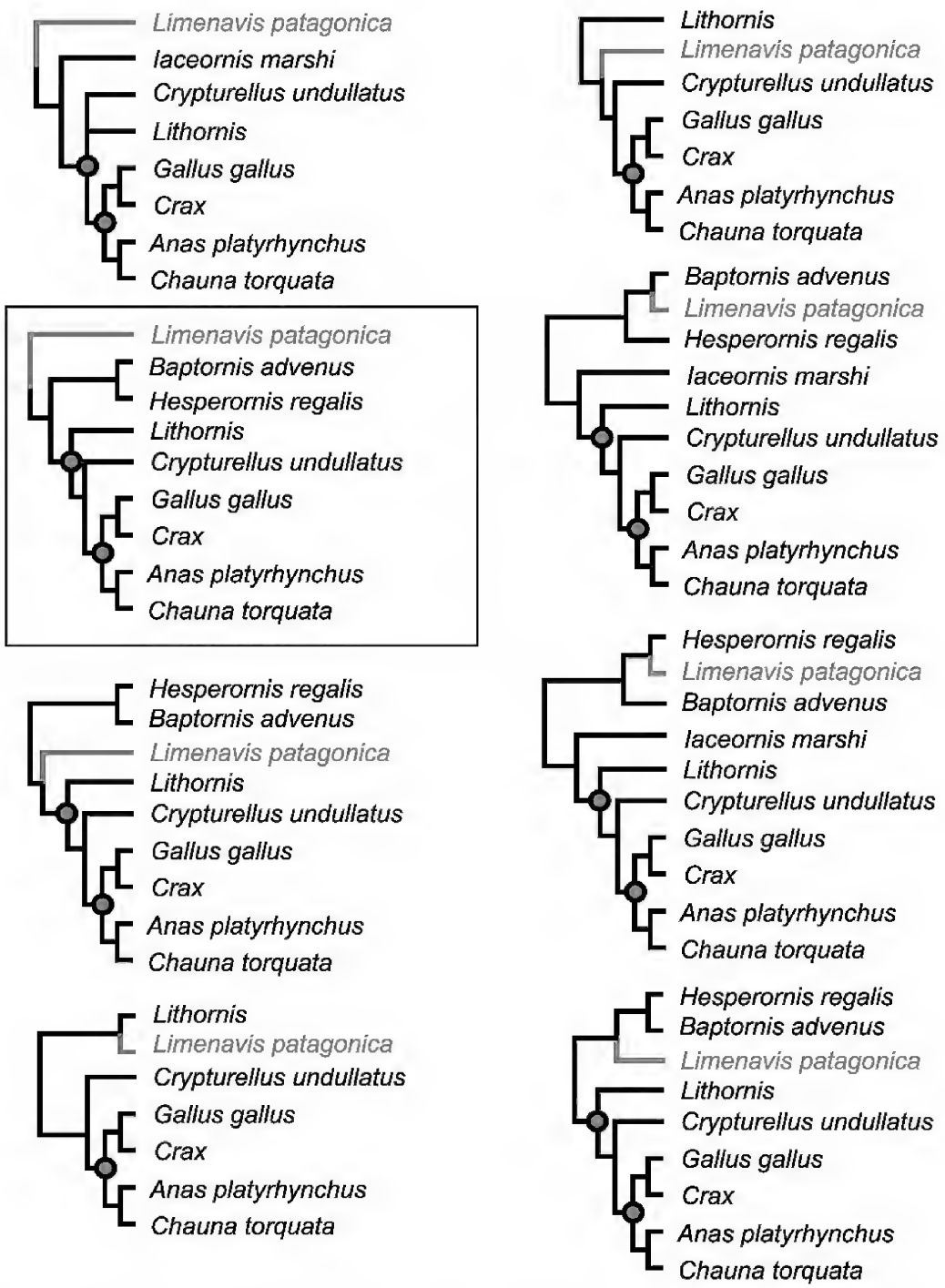


Fig. 60. Cladograms illustrating the eight alternate positions that *Limenavis patagonicus* can take in the most parsimonious set of trees. Topology highlighted in the box is the only one with unambiguous support of the position of *Limenavis patagonicus*.

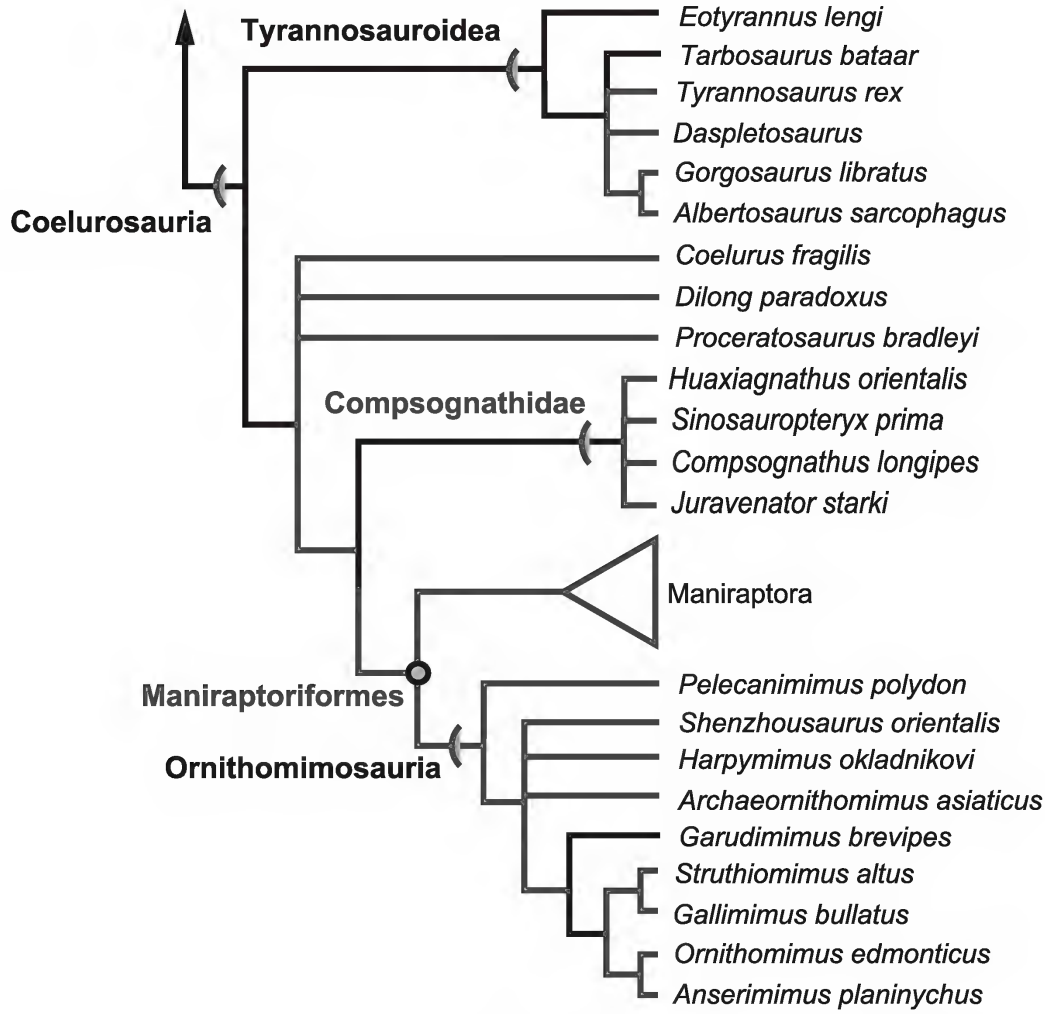


Fig. 61. Reduced strict consensus cladogram of basal coelurosaur relationships. Maniraptoran taxa have been collapsed into a single terminal.

Coelurosauria, notably Tyrannosauroidea, *Proceratosaurus bradleyi*, *Dilong paradoxus*, *Pelecanimimus polydon*, and *Ornitholestes hermanni*. Coelurosaurs including and more derived than the node marked by the common ancestor of Alvarezsauroidea + Therizinosauria + Oviraptorosauria + Paraves exhibit a reversal to the plesiomorphic subcircular morphology, with some modifications to spatulate teeth in some therizinosaurs and extremely modified unusual teeth in basal oviraptorosaurs.

In the postcranial skeleton the cervical and anterior trunk vertebrae are amphiplatyan (char. 101.0) compared to the opisthocoelous vertebrae seen in the proximate outgroups. Noted by Gauthier (1986), this feature has remained a consistent synapomorphy for Coelurosauria (Holtz, 1998; Norell et al., 2001; Hwang et al., 2004b; Makovicky et al., 2005; Turner et al., 2007a). Derived alvarezsaurids, however, exhibit a reversal to the plesiomorphic opisthocoelous condition, whereas in ornithurines and a few basal euornithines exhibit further transformation to a heterocoelous condition.

In non-coelurosaurian tetanurans, the ascending process of the astragalus is confluent with the condylar portion. In coelurosaurs, the condylar portion and the ascending process are separated by a transverse groove

(in more basal coelurosaurs like tyrannosauroids and ornithomimosaurs) or a well-defined fossa (as in maniraptorans) (char. 197.1). In the pelvis, coelurosaurs share a triangular obturator process on the ischium, the caudal portion of which is confluent with the shaft of the ischium (char. 233.1). This feature was noted as a synapomorphy for coelurosaurs by Sereno (1999: char. 43) and later incorporated into the TWiG matrix by Makovicky et al. (2005: char. 233). Some specimens of *Sinosauropteryx* and some derived therizinosaurs, however, exhibit a reversal to the quadrangular obturator process of more basal tetanurans (Currie and Chen, 2001).

Unnamed Clade (Compsognathidae + Maniraptoriformes)

This group is united by four unambiguous synapomorphies. Ancestrally adult members of this group possess a lacrimal that lacks a supraorbital crest (char. 37.0), although a reversal to some degree of lacrimal crest is present in *Shuvuuia deserti*, all troodontids more derived than *Anchiornis huxleyi*, and some derived ornithurines. Likewise members of this group lack an enlarged foramen or foramina at the angle of the lacrimal above the antorbital fenestra (char. 38.0). A reversal to the presence of a foramen is seen in the dromaeosaurid *Austroraptor cabazai* and the oviraptorosaurs *Rinchenia* and *Citipati*. The antitrochanter on the ilium, located posterior to the acetabulum, is prominent in members of this clade (char. 162.1). Among compsognathids this feature is scorable only in *Juravenator starki,* but is then widespread among maniraptoriforms. Reversals to a more weakly developed antitrochanter are seen in *Archaeornithomimus*, *Haplocheirus*, *Segnosaurus*, *Anchiornis*, *Sapeornis*, and *Cathayornis*. Lastly, the supratemporal fossa has only a limited extension onto the dorsal surfaces of the frontal and postorbital (char. 245.0). This is reversed in most dromaeosaurids, *Citipati*, and IGM 100/1126.

Maniraptoriformes Holtz, 1995

Definition: A node-based monophyletic group containing *Passer domesticus* (Linnaeus, 1758), *Ornithomimus edmontonicus* Sternberg, 1933, and all their descendents.

A total of seven unambiguous synapomorphies united this clade, but overall nodal support remains relatively low (see below). Four cranial characters are shared among the coelurosaurs in this group, including the absence of a jugal recess in the posteroventral corner of the antorbital fossa (char. 33.1), the absence of a coronoid ossification (char. 76.2), the absence of distinct interdental plates (char. 90.0)—reversed in some therizinosaurs and *Archaeopteryx lithographica*, and the quadrate cotyle of the squamosal is open laterally exposing the quadrate head (char. 216.1). Postcranially, maniraptoriforms have cervical epipophyses placed proximal to the postzygapophyseal facets (char. 95.1) and broad and short cervical ribs (char. 124.1). In lateral view, the coracoid has a shallow ventral blade with an elongate posteroventral process (char. 136.2), which becomes further modified in more derived maniraptorans and avialans.

Maniraptora Gauthier, 1986

Definition: A stem-based monophyletic group containing *Passer domesticus* (Linnaeus, 1758) and all coelurosaurs closer to it than to *Ornithomimus edmontonicus* Sternberg, 1933.

In Gauthier's formulation (Gauthier, 1986), as followed above, this group contained all coelurosaurs more derived than ornithomimosaurs. He considered *Compsognathus longipes*, *Coelurus fragilis,* and *Ornitholestes hermanni* as likely members of this group. Holtz (1998), however, failed to recover either *Ornitholestes* or *Coelurus* as maniraptorans. Sereno (1997, 1999) likewise did not find *Ornitholestes* as a maniraptoran, but did not consider *Coelurus* in his analysis. Makovicky and Sues (1998) found both *Ornitholestes hermanni* and *Coelurus fragilis* as maniraptorans.

All TWiG matrices (e.g., Norell et al., 2001; Hwang et al., 2002; Makovicky et al., 2003; Hwang et al., 2004b; Xu and Norell, 2004; Makovicky et al., 2005; Norell et al., 2006; Turner et al., 2007a, 2007c) have found *Ornitholestes* as a maniraptoran except that

by Turner et al. (2007b), where its position was unresolved. All TWiG matrices that included compsognathids (Hwang et al., 2004b; Xu and Norell, 2004; Makovicky et al., 2005; Norell et al., 2006; Turner et al., 2007a, 2007c) recover compsognathids as maniraptorans again except that by Turner et al. (2007b) in which they were basal to the Ornithomimosauria-Maniraptora split. The only TWiG matrices to include *Coelurus fragilis* previous to this study were those by Turner et al. (2007b) and Makovicky et al. (2009), both of which found it outside Maniraptora and Maniraptoriformes. Senter (2007), which is based largely on the TWiG backbone with many characters from Holtz (1998), finds *Ornitholestes* as a maniraptoran, but *Coelurus* and compsognathids as non-maniraptorans. Zanno et al. (2009) and Zanno (2010a) use the TWiG matrix as a backbone and both analyses found *Coelurus* and *Ornitholestes* as maniraptorans and compsognathids outside Maniraptora. Conversely, the recent analysis of Choiniere et al. (2010), also using TWiG as a backbone, recovered *Ornitholestes* and compsognathids as maniraptorans, but *Coelurus* very basal among coelurosaurs.

The present analysis finds *Ornitholestes* as the basalmost maniraptoran (fig. 62), but *Coelurus* located more basally among coelurosaurs (although not as basal as the analysis of Choiniere et al., 2010). Four synapomorphies unite *Ornitholestes* with all other maniraptorans. These include a quadratojugal with a horizontal process posterior to the ascending process forming an inverted T or Y shape (char. 35.1)—reversed in *Archaeopteryx*, *Mei*, *Sinornithoides*, *Utahraptor*, *Citipati*, *Rinchenia*, *Conchoraptor*, and *Incisivosaurus*—and the lateral border of the quadrate shaft possesses a broad, triangular process along the lateral edge of the shaft that contacts the squamosal and the quadratojugal above an enlarged quadrate foramen (char. 53.1)—reversed in most troodontids, *Incisivosaurus*, and avialans. Additionally, a short and deep paroccipital process with a convex distal end (char. 56.1) and anterior trunk vertebrae with large hypapophyses (char. 102.1) also characterize maniraptorans.

Unnamed Clade (Alvarezsauroidea + Therizinosauria + Oviraptorosauria + Paraves)

Perle et al. (1994), Chiappe et al. (1996, 1998), Novas (1997), and Holtz (1998) found alvarezsaurids close to Avialae (Metornithes). Subsequent analyses including Sereno (1999) and all versions of the TWiG matrix (Norell et a., 2001; Novas and Pol, 2002; Hwang et al., 2002; Makovicky et al., 2003; Hwang et al., 2004b; Makovicky et al., 2005; Norell et al., 2006; Turner et al., 2007a, 2007b) place alvarezsaurids in a more basal position, with Sereno (1999) finding an ornithomimosaur + alvarezsaurid clade, although this topology has not been supported in any subsequent phylogenetic analysis. Senter (2007) also recovers this group but with slightly different interrelationships among the constituent clades, as do Zanno et al. (2009), Zanno (2010a), and Choiniere et al. (2010).

In our study, this derived maniraptoran clade is supported by 12 unambiguous synapomorphies and considerable nodal support (see below). In this clade the frontal process of the postorbital in lateral view curves anterodorsally with the dorsal border of temporal bar concave (char. 4.1). The maxillary process of the premaxilla is reduced, so that the maxilla participates broadly in external naris (char. 20.1), although this is reversed in oviraptorosaurs and ornithurines to the plesiomorphic condition, whereas in derived Laurasian dromaeosaurids it is even further transformed. Fused parietals (char. 46.1), maxillary and dentary teeth without serrations anteriorly (char. 83.1), and premaxillary tooth crowns suboval to subcircular in cross section (char. 91.0) also optimizes at this node.

Two characters supporting the group have been found in previous versions of TWiG. The teeth are constricted between root and crown (char. 88.0), and prezygapophyses are reduced on the distal caudal vertebrae (char. 120.2). This last character is a reversal of the plesiomorphic elongate state in basal avialans more derived than *Archaeopteryx lithographica* and are further transformed into the hyperelongate prezygapophyses characteristic of a subset of dromaeosaurid taxa more derived than *Mahakala omnogovae*.

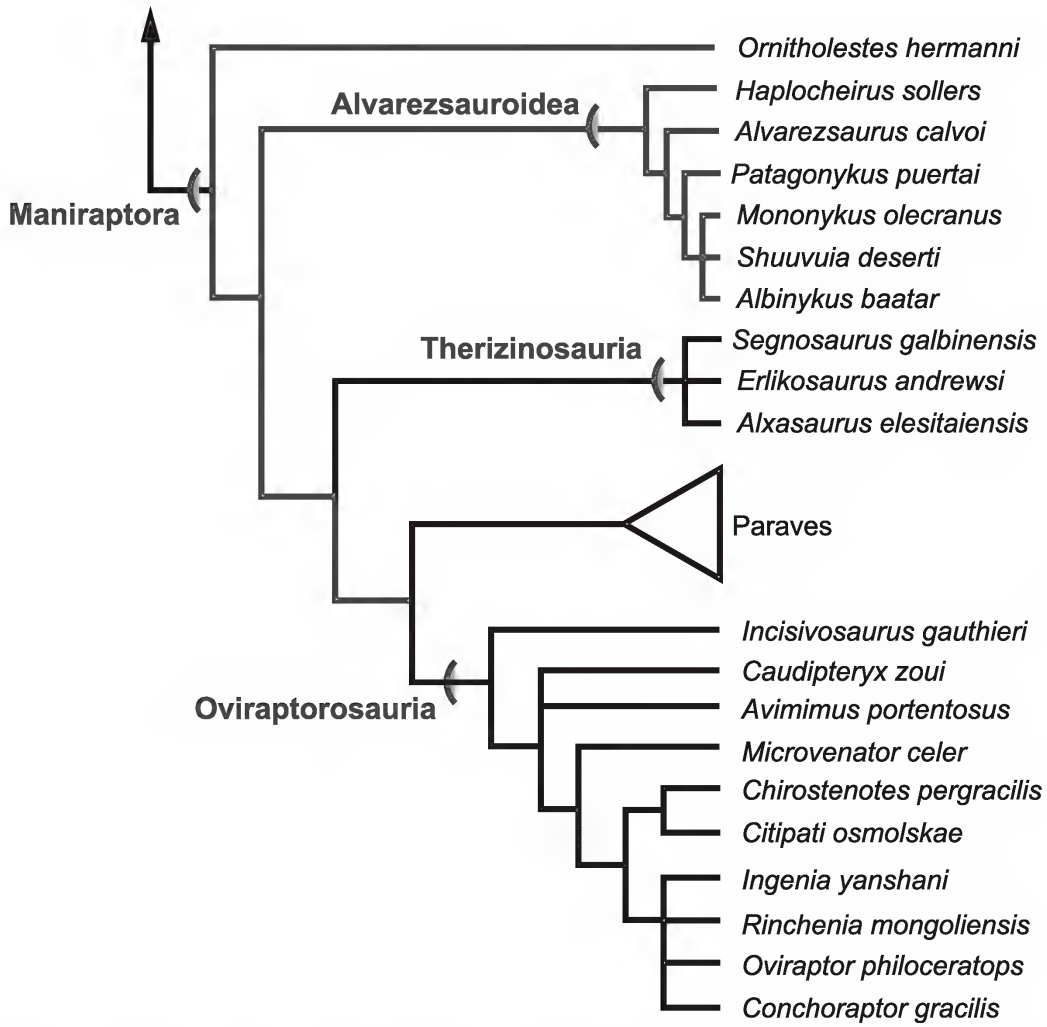


Fig. 62. Reduced strict consensus cladogram illustrating the relationships among nonparavian maniraptorans. Paravian taxa have been collapsed into a single terminal.

A number of pelvic transformations also support this clade. The supraacetabular crest on the ilium is reduced at this point on the coelurosaur tree and does not form a hood over the acetabulum (char. 157.1). The brevis fossa becomes shelflike (char. 161.0) and well developed along the full length of postacetabular blade with the lateral overhang extending along full length of the fossa, completely covering the medial edge when viewed laterally (char. 217.1). The distal ends of the ischia approach one another, but do not form a symphysis (char. 174.1).

Lastly, an unkinked pterygoid with the braincase articulation inline with the main axis of the bone (char. 339.1) optimizes at this node. The character is unknown for many coelurosaurs and is highly homoplastic among nonavialan coelurosaurs where it can be observed. A reversal to a kinked morphology is present in nearly all paravians excluding crown-group Aves.

Unnamed Clade (Therizinosauria + Oviraptorosauria + Paraves)

This clade was not present in Holtz (1998), Sereno (1999), or in the more recent analyses by Senter (2007), Zanno et al. (2009), and Hu et al. (2009), with the latter three finding

therizinosaurs to occupy a more basal position. In the case of Holtz (1998) this group was not recovered because alvarezsaurids were found nested up the tree with avialans and in Sereno (1997) and Sereno (1999) therizinosaurs were found closely related to Ornithomimosaurs. A Therizinosauria + Oviraptorosauria + Paraves clade was recovered by Makovicky and Sues (1998), Norell et al. (2001), Makovicky et al. (2005), Norell et al. (2006), Turner et al. (2007a, 2007b), but remained unresolved in Hwang et al. (2004b) because of a lack of consensus in the position of alvarezsaurids. Kirkland et al. (2005) also recovered a large polytomy at the base of Maniraptora, whereas Zanno et al. (2009) recovered oviraptorosaurs as the sister taxon to Paraves and alvarezsaurids occupying the next position just outside this group. The phylogenetic analysis of Hu et al. (2009), which is largely based on the dataset of Senter (2007), also finds this topology. The strict consensus of Choiniere et al. (2010) depicts a polytomy between therizinosaurs, oviraptorosaurs, alvarezsauroids, and paravians. Two alternate most parsimonious topologies are present—one that mimics the relationships recovered in the present study with alvarezsauroids basal to therizinosaurs + oviraptorosaurs + paravians and a second topology with therizinosaurs + oviraptorosaurs sister to an alvarezsauroid + paravian clade.

Two cranial synapomorphies support this grouping, one is the absence of a basisphenoid recess (char. 9.2), although this is reversed in oviraptorosaurs, basal therizinosaurs, and derived Laurasian dromaeosaurids, and the other is a downturned symphyseal end of the dentary (char. 66.1). The downturned dentary optimizes at this node because of the condition present in oviraptorosaurs, therizinosaurs, and *Epidexipteryx*. Maniraptorans more derived than the *Epidexipteryx* node show a reversal to the plesiomorphic straight dentary morphology.

Therizinosaurs, oviraptorosaurs, and paravians all possess a coracoid that in lateral view is subquadrangular with an extensive ventral blade (char. 136.1). Likewise members of this clade possess a proximodorsal "lip" on some manual unguals (char. 153.1). The supraacetabular crest on the ilium is further reduced from the ancestral maniraptoran condition and is altogether absent (char. 157.2). The ischial shaft in these taxa is wide, flat, and platelike (char. 166.1).

Unnamed Clade (Oviraptorosauria + Paraves)

Seven synapomorphies unite Oviraptorosauria with Paraves. Four of these synapomorphies pertain to changes in cranial morphology. The quadratojugal lacks a horizontal process posterior to the ascending process forming an L-shaped quadratojugal (char. 35.0). Unfortunately, the feature is not known for many paravians and shows a reversal to a T-shaped morphology in most dromaeosaurids. The prefrontal is absent in members of this clade (char. 40.2) (except some specimens of *Deinonychus* and in *Sinornithosaurus*) and the dorsal surface of the parietals is dorsally convex with a very low sagittal crest along the midline (char. 45.1). The coronoid ossification is expressed as a thin splint of bone in members of this clade (and completely lost in *Archaeopteryx lithographica*) (char. 76.1) and the squamosal overhangs the quadrate cotyle and covers the head of the quadrate in lateral view (char. 216.0).

In the axial skeleton, members of this clade exhibit short, wide, and slightly inclined transverse processes of the anterior dorsal vertebrae (char. 107.1). This feature is shared convergently with the basal alvarezsauroid *Haplocheirus sollers* and is reversed in derived Laurasian dromaeosaurids and *Microraptor zhaoianus* to the plesiomorphic long and thin condition.

The presence of a semilunate carpal (a single distal carpal present capping all or portions of metacarpals I and II) diagnoses this clade (char. 146.1). The presence of a semilunate carpal in theropods more basal than this node is problematic. The semilunate carpal identified by Hwang et al. (2004b) in *Huaxiagnathus orientalis* is reinterpreted here to be a large distal carpal I and the ulnare of those same authors is reinterpreted to be a much smaller distal carpal II. This is a similar configuration to that present in *Allosaurus fragilis* (Chure, 2001). *Coelurus fragilis* has a large "semilunate" carpal that is very similar

to that seen in members of the Oviraptorosauria + Paraves clade. However, the distal articulation surface is angled (like that in carpal I of *Allosaurus*) and not flat like those one sees in the semilunate carpal of derived paravians like *Velociraptor*. It is preserved in isolation from the other manual elements, so it is ambiguous whether this represents a true semilunate carpal homologous with that present in this clade or it is like more basal tetanurans that have an enlarged distal carpal I. In the present analysis, this feature was scored as unknown (?) in *Coelurus fragilis,* but this may prove to be homologous and therefore a possible feature drawing *Coelurus* up-tree into a topology similar to that recovered by Makovicky and Sues (1998), Zanno et al. (2009), and Zanno (2010a). The carpal of *Coelurus* is very similar to the distal carpal I in *Falcarius* (Zanno, 2010b), which in some individuals fuses to distal carpal II to form a true semilunate carpal. This suggests that the correct interpretation of the *Coelurus* carpal in question is that it is a distal carpal I. Whether this carpal fused to distal carpal II is unknown. The inclusion of *Falcarius* in the present dataset could result in this character optimizing at a different position on the tree or it may be that some version of a partially fused "semilunate" carpal complex is characteristic of a more inclusive coelurosaur clade.

Paraves Sereno, 1997

Definition: A stem-based monophyletic group containing *Passer domesticus* (Linnaeus, 1758) and all coelurosaurs closer to it than to *Oviraptor philoceratops* Osborn, 1924 (sensu Holtz and Osmólska, 2004).

Beginning with Ostrom's (1969a) work documenting the morphological similarities between the dromaeosaurid *Deinonychus antirrhopus* and *Archaeopteryx lithographica* specifically and birds generally, taxa that today constitute Paraves have been grouped in close phylogenetic association. Gauthier (1986) recovered a Dromaeosauridae + Troodontidae + Avialae clade as did many subsequent analyses (e.g., Sereno, 1997, 1999; Makovicky and Sues, 1998; Xu et al., 1999, 2000; Hwang et al., 2002; Makovicky et al., 2003; Hwang et al., 2004b; Xu and Norell, 2004; Makovicky et al., 2005; Novas and Pol, 2005; Norell et al., 2006; Turner et al., 2007a, 2007b, 2007c). Studies that have failed to recover this clade (e.g., Holtz, 1998, 2001; Senter et al., 2004) do so because the troodontids sampled in their datasets group with ornithomimids. This clade was not found by Senter in his more recent analysis (Senter, 2007) and has been convincingly demonstrated to be the result of attraction between convergent branches because of insufficient taxon sampling at the base of Troodontidae and Ornithomimosauria (Makovicky et al., 2003).

In the present analysis, *Epidexipteryx hui* is recovered as the basalmost paravian outside the split between the traditional paravian clades Avialae and Deinonychosauria. This result is interesting because it departs from previous phylogenetic work suggesting *Epidexipteryx* is a basal avialan. The basal position of *Epidexipteryx* results in low nodal support for paravian monophyly (see below) and a novel set of synapomorphies supporting the clade. These features include large dentary and maxillary teeth (char. 84.1), the posterolateral surface of the coracoid ventral to the glenoid fossa is expanded to form a triangular subglenoid fossa bounded laterally by an enlarged coracoid tuber (char. 134.1), a humerus that is longer than the scapula (char. 139.1), a calcaneum and astragalus that are fused to each other but not to the tibia (char. 198.1), and the position of the frontoparietal suture is at the level of the postorbital process of the frontal (char. 464.1).

Paraves, exclusive of *Epidexipteryx hui*, is much better supported with high GC values, three unambiguous synapomorphies and six ambiguous synapomorphies. These six ambiguous synapomorphies (chars. 137.1, 144.1, 156.1, 160.1, 414.0/1, and 474.1) are unknown in *Epidexipteryx* and may ultimately optimize along the Paraves stem. They are discussed here because they have important evolutionary implications and entail the more traditional suite of paravian characteristics.

Paraves, exclusive of *Epidexipteryx hui*, is marked by a suite of modifications to the shoulder girdle typically associated with the origin of the "avian" flight stroke (Ostrom, 1976b; Jenkins, 1993). The acromion margin of the scapula has a laterally everted anterior edge (char. 133.1) (fig. 55), the coracoid is

inflected medially from the scapula forming an L-shaped scapulocoracoid in lateral view (char. 137.1) and the glenoid fossa faces laterally (char. 138.1) as opposed to the plesiomorphic posterior orientation (fig. 50). Additionally, the furcula is nearly symmetrical in shape as opposed to the asymmetry present in the furcula of more basal taxa (char. 474.1). The scapular acromion is the origin site of the m. deltoideus clavicularis (= m. propatagialis in Aves) (Meers, 2003; Baumel and Witmer, 1993; Jasinoski et al., 2006). Ancestrally this muscle served to protract and abduct the humerus. This eversion of the acromion in paravians may relate to a partial reorganization of the muscle orientation or served to increase the surface area of attachment. The L-shaped scapulocoracoid represents an incipient stage of the enhanced bracing of the shoulder girdle where the coracoids have an extensive anterior contact with the ossified sternum, while the scapulae take a more dorsally displaced position on the back, paralleling the vertebral column. This modification also results in a partial reorientation of the glenoid such that the short axis is inclined vertically (although not completely vertical) and that ancestral protraction-retraction movement of the humerus across this joint results in partial elevation-depression (Jenkins, 1993). Along with this modification, the laterally oriented glenoid allows the humerus to be abducted to a greater degree than in more basal coelurosaurs, although still probably not greatly above horizontal. Early analyses of these morphological modifications and/or coelurosaur phylogeny placed these changes at the avialan node (Sereno, 1997, 1999; Jenkins, 1993), but it is now clear that they are paravian synapomorphies.

Troodontids, dromaeosaurids, and avialans all share a dentary symphyseal region that is in line with the main part of the buccal margin (char. 66.0), i.e., the symphysis is not downturned as in oviraptorosaurs, therizinosaurs, and *Epidexipteryx*. In paravians, but unknown in *Epidexipteryx*, the proximal surface of ulna is divided into two distinct fossae separated by a median ridge (char. 144.1) (fig. 46). This feature may in fact have a broader distribution, but the proximal surface of the ulna is poorly known in oviraptorosaurs and is heavily modified in alvarezsaurids. Ancestrally in paravians, the anterior end of the ilium is strongly convex or lobate (char. 156.1) (fig. 55). This is in contrast to the slightly rounded to straight anterior edge present in non-tyrannosaurid coelurosaurs, although some derived euornithines revert to the plesiomorphic rounded anterior edge whereas Laurasian dromaeosaurids (i.e., Velociraptorinae + Dromaeosaurinae) have a pointed anterodorsal corner with a concave anteroventral edge.

Along the dorsal edge of the ilium, paravians possess a distinct tuber (or processus supratrochantericus) (char. 160.1) (figs. 18, 55). This process is often associated with an oblique ridge dividing the lateral surface of the ilium (Hutchinson, 2001a; Vanden Berge and Zweers, 1993). This ridge marks the division between the origin of m. iliofemoralis externus and the m. iliofibularis. The oblique ridge serves a role similar to that of the "vertical ridge" present in tyrannosauroid ilium—namely the division of the preacetabular concavity from the postacetabular concavity. We follow the conclusion of Hutchinson (2001a) and do not consider the "vertical ridge" and the oblique ridge below the supratrochanteric process homologous. Numerous tests of congruence reject this hypothesis as well as incomplete satisfaction of the connectivity criterion (e.g., no supratrochanteric process in Tyrannosauroidea).

The femora of paravians possess a distinct posterior trochanter (char. 414.0/1) (fig. 18). Ostrom (1976a) described this feature in *Deinonychus antirrhopus* noting that it coincided with the insertion of the m. ischiofemoralis. This trochanter is a rounded prominent tubercle among basal paravians, while in euornithines it is further derived into a hypertrophied shelflike structure (Hutchinson, 2001b).

Deinonychosauria Colbert and Russell, 1969

Definition: A node-based monophyletic group containing the last common ancestor of *Troodon formosus* Leidy, 1856, and *Velociraptor mongoliensis* Osborn, 1924, and all of its descendants (sensu Sereno, 1998).

Since Deinonychosauria was erected by Colbert and Russell (1969) the group has been primarily characterized by a distinctive foot morphology comprised of a highly modified, raptorial digit II (fig. 2), exhibited to various degrees in both dromaeosaurids and troodontids. Both Colbert and Russell (1969) and Ostrom (1969a) discussed the great similarity between the dromaeosaurids and troodontids known at the time, but neither explicitly included troodontids in Deinonychosauria. Gauthier (1986) explicitly discussed Deinonychosauria in terms of including both Dromaeosauridae and Troodontidae.

Numerous authors have raised doubts regarding Deinonychosaurian monophyly. These include Barsbold (1983a), Currie (1987), Osmólska (1981), Osmólska and Barsbold (1990), Currie and Zhao (1993), Currie (1995), and even Gauthier (1986) in the addendum at the end of the paper (Gauthier, 1986: 48). With subsequent discoveries of new dromaeosaurids and troodontids, coupled with newer and more comprehensive phylogenetic analyses, Deinonychosauria is now a well-supported clade.

Beyond the characteristic pedal morphology, eight synapomorphies are present throughout the skeleton. In deinonychosaurs the anterodorsal process of the lacrimal is much longer than the posterior process (char. 39.2). This feature in reversed in microraptorine, dromaeosaurine, and velociraptorine dromaeosaurids. The occurrence of this feature in *Austroraptor* is what results in this feature optimizing as a deinonychosaur synapomorphy as opposed to a troodontid synapomorphy. The pterygoid flange is well developed (char. 61.0) unlike the poorly developed pterygoid flange seen in all other maniraptorans. Nutrient foramina on the external surface of the dentary lie within a deep groove ancestrally for deinonychosaurs (char. 71.1). This feature was previously interpreted as convergently shared between unenlagiine dromaeosaurids and troodontids but currently optimizes at Deinonychosauria. This feature is reversed in dromaeosaurids more derived than Unenlagiinae. A large surangular foramen is present in deinonychosaurs (char. 74.1) (figs. 10, 38). This feature is present primitively for coelurosaurs, but is absent in *Proceratosaurus bradleyi*, *Dilong paradoxus*, and *Ornitholestes hermanni* and small in ornithomimosaurs. A surangular foramen is present in *Compsognathus longipes*, but absent in alvarezsaurids (*Shuvuuia deserti* IGM 100/977), Oviraptorosauria + Therizinosauria, and most avialans—*Sapeornis chaoyangensis* IVPP V13396 and *Confuciusornis sanctus* IVPP V11374 convergently possess a surangular foramen.

The splenial in deinonychosaurs is uniquely exposed as a broad triangle between dentary and angular visible on the lateral surface of the mandible (char. 75.1) (fig. 38). Currently, only in deinonychosaurs (and convergently in *Conchoraptor gracilis*) do the scars for the interspinous ligaments terminate below the apex of the neural spine (char. 109.1) as opposed to the plesiomorphic condition where the scars are present up to the apices of the neural spine. The distribution of this plesiomorphic condition, however, is poorly known among nonparavian coelurosaurians, particularly in avialans, compsognathids, and alvarezsaurids. The plesiomorphic state is known to be present in *Ornitholestes hermanni* AMNH FARB 619 and *Coelurus fragilis* YPM 2010.

The characteristic ungual and penultimate phalanx of pedal digit II that is highly modified for extreme hyperextension (char. 204.1) (fig. 40), not unexpectedly, continues to optimize as a Deinonychosauria synapomorphy. This complex consists of a shortened phalanx II-2 with a prominent proximal ventral flexor heel and a distal end with a large and deeply grooved ginglymoid articular facet. This surface extends ventrally far past the proximal extent of the dorsal limit. The ungual for this digit is more strongly curved and significantly larger than that of digit III (see Discussion below for an analysis of this supposed condition in *Archaeopteryx*). Lastly, in deinonychosaurs the bicipital scar is developed as a slightly raised scar (char. 384.1) (fig. 46). A bicipital scar is convergently shared with pygostylian avialans and is particularly well developed in Ornithurae.

Troodontidae Gilmore, 1924

Definition: A stem-based monophyletic group containing *Troodon formosus* Leidy,

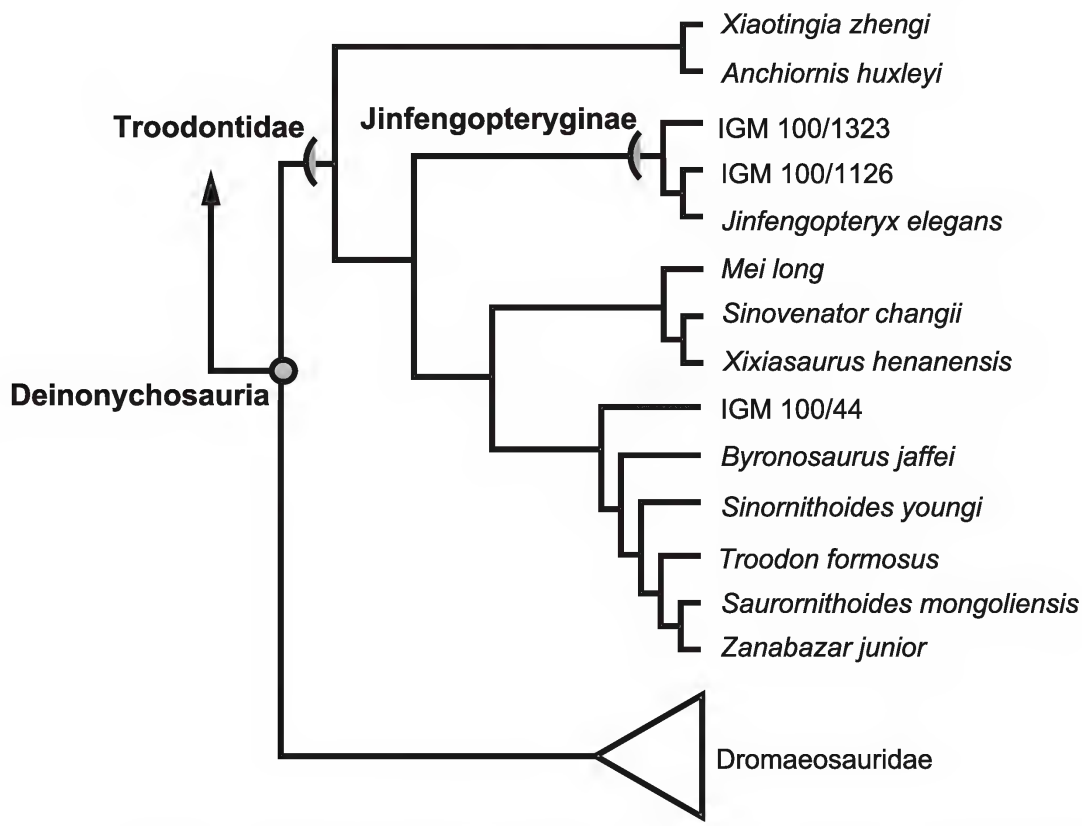


Fig. 63. Strict consensus cladogram illustrating the troodontid relationships. Dromaeosaurid taxa have been collapsed into a single terminal.

1856, and all coelurosaurs closer to it than to *Velociraptor mongoliensis* Osborn, 1924, or *Passer domesticus* (Linnaeus, 1758) (sensu Sereno, 1998).

Troodontidae (fig. 63) is moderately well supported in this analysis. Because of the increased taxon sampling and addition of five new basal troodontids, most of the characters identified by Makovicky et al. (2003) as synapomorphic for Troodontidae are here found to characterize less inclusive troodontid clades. The phylogeny of Troodontidae is currently under investigation (R. Pei, personal commun.), so conclusions reached here are preliminary.

Currently, three unambiguous synapomorphies support Troodontidae with *Anchiornis huxleyi* + *Xiaotingia zhengi* as its basalmost clade. The internarial bar is flat in cross section (char. 21.1). The quadrate is strongly inclined anteroventrally, so that the distal end lies far forward of the proximal end (char. 51.1), a feature shared convergently with *Sinosauropteryx*, *Struthiomimus*, *Gallimimus*, *Ornithomimus*, *Erlikosaurus*, and *Incisivosaurus*.

The discovery of *Sinovenator changii* (Xu et al., 2002a) appeared to provide a transitional morphology of a partially arctometatarsalian condition (like that in *Sinovenator*) to the more extreme constriction seen in all other troodontids (except *Sinornithoides*). However, with the inclusion of *Anchiornis*, IGM 100/1323, and IGM 100/1126 and recognition of these specimens as basal troodontid taxa, the subarctometatarsalian condition in *Sinovenator* seems to be a partial reversal from an ancestral metatarsal III proximal shaft that is very pinched and not exposed along the proximal section of the metapodium (arctometatarsal: char. 203.2).

Unnamed Clade (*Anchiornis huxleyi* + *Xiaotingia zhengi*)

Five characters unambiguously support this novel clade of Late Jurassic Chinese troodontids. Two features in the maxilla unite this clade. These include the presence of a tertiary antorbital fenestra (promaxillary fenestra) (char. 29.1) and the lateral lamina of the ventral ramus of the nasal process of the maxilla is reduced to a small triangular exposure (char. 244.1). The former feature is shared convergently with a number of other paravians including *Xixiasaurus*, *Sinovenator*, non-unenlagiine dromaeosaurids, and *Archaeopteryx*. The latter feature is also present among other paravians, including *Jinfengopteryx*, IGM 100/1126, *Sinovenator*, *Microraptor*, *Sinornithosaurus*, *Bambiraptor*, and *Shanag*.

The ridge bounding the cuppedicus fossa extends far posteriorly and is almost confluent with the acetabular rim (char. 163.1) in *Anchiornis* and *Xiaotingia* and is shared convergently with the microraptorine *Tianyuraptor* and the unenlagiines *Rahonavis* and *Unenlagia*. Additionally, metatarsal I articulates to the posterior surface of the distal quarter of metatarsal II (char. 205.1) and the neural spines on the posterior dorsal vertebrae are anteroposteriorly expanded distally in lateral view (char. 209.1).

Unnamed Clade (Jinfengopteryginae + *Sinovenator* + *Mei* + *Xixiasaurus* + IGM 100/44 + *Byronosaurus* + *Sinornithoides* + *Troodon* + *Saurornithoides* + *Zanabazar*)

Nine characters unambiguously support the clade along with a moderate jackknife value. Troodontids more derived than *Anchiornis* have a well-developed supraorbital crest on the lacrimal that takes the form of a large lateral expansion anterior and dorsal to the orbit (char. 37.2). This feature is unique to the clade among nonavian theropods although it is convergently present in some paleognaths and galloanseriforms.

The foramen magnum is oval shaped in troodontids being taller than wide (char. 54.1). This is reversed, however, in *Troodon formosus*. Numerous dentary teeth diagnose this clade (char. 84.1). Dentary tooth size is a very homoplastic character. A number of other maniraptorans have numerous small teeth (e.g., therizinosaurs, *Haplocheirus*, *Shuvuuia*, *Pelecanimimus*, and unenlagiine dromaeosaurids).

The neural spines on the distal caudals are absent and midline sulci are instead present centered on the neural arches (char. 119.2)—a feature completely unique to troodontids. Troodontids more derived than *Anchiornis* have a scapula that is longer than the humerus (139.0), but this feature is unknown in many derived troodontids. The asymmetrical foot discussed by Makovicky et al. (2003) with slender metatarsal II and very robust metatarsal IV (chars. 208.1 and 434.2) now diagnoses this clade of troodontids although it is paralleled in *Microraptor*. Additional synapomorphies of the pes include a metatarsal II that is shorter than metatarsal IV (char. 438.1/2) and a pedal phalanx II-2 with a distal articular surface less than half the size of the proximal surface (char. 456.1—reversed in *Sinovenator changii*).

Jinfengopteryginae, new clade name

Definition: A stem-based monophyletic group containing *Jinfengopteryx elegans* Ji et al., 2005, and all coelurosaurs closer to it than to *Troodon formosus* Leidy, 1856, *Passer domesticus* (Linnaeus, 1758), and *Sinovenator changii* Xu et al., 2002.

We name this new clade of troodontids for two reasons. First, the clade represents a distinct group that is the sister taxon to nearly all other troodontids, therefore having a specific name for this group serves a practical purpose in discussions of troodontid relationships and evolution. Second, the clade possesses strong character support (six unambiguous synapomorphies) and high jackknife support, rendering it relatively stable. A stem-based clade name was chosen in order to provide a taxonomic framework for additional troodontid taxa that may be found or are undescribed and prove to be close relatives to this basal troodontid clade.

Jinfengopterygines are diagnosed by an enlarged and pronounced round accessory antorbital fenestra (maxillary fenestra) that takes up most of the space between the

anterior margins of the antorbital fenestra and fossa (char. 27.2). The presence of a maxillary fenestra is common to most coelurosaurs, although pygostylians represent a derived reversal to an absence of this structure. This enlarged and somewhat triangular maxillary fenestra is unique to jinfengopterygines. In addition to its shape, the maxillary fenestra is also situated at the rostral border of the antorbital fossa in jinfengopterygines (char. 28.0). This is the ancestral condition for Maniraptora; however, paravians show a shift in the location of the maxillary fenestra away from the anterior border of the antorbital fossa.

The lacrimal in jinfengopterygines shows an apomorphic reversal to a T-shaped outline in lateral view because an anterodorsal process that is equal in length to the posterior process (char. 39.1). This feature is shared convergently with *Archaeopteryx*, *Pengornis*, *Mei*, *Incisivosaurus*, and Laurasian dromaeosaurids.

Ancestrally for paravians the ischium is considerably shorter than the pubis. This is the case for non-euornithine avialans, all non-jinfengopterygine troodontids, and dromaeosaurids (except *Achillobator*). In Jinfengopteryginae the ischium secondarily reverts to being more than 2/3 the length of the pubis (char. 173.0). The pubic apron is less than 1/3 shaft length (char. 181.1) in this clade, a feature shared convergently with avialans and derived oviraptorosaurs and *Patagonykus puertai*.

Completely unique to this subclade of troodontids is a jugal with the sublacrimal part bifurcated anteriorly (char. 262.3). In the pes of jinfengopterygines, metatarsal III is displaced plantarly at its proximal end relative to the position of metatarsals II and IV (char. 428.1). This feature is shared convergently with all euornithines more derived than *Patagopteryx* and *Hongshanornis*.

Unnamed Clade (IGM 100/1126 + *Jinfengopteryx*)

The sister-group relation of these two taxa to the exclusion of IGM 100/1323 is supported by the reduction of the lateral lamina of the ventral ramus of the nasal process of the maxilla to a small triangular exposure (char. 244.1). This is paralleled in *Sinovenator changii* and *Sinornithosaurus millenii*, *Microraptor zhaoianus*, *Shanag ashile,* and the basal avialan *Jeholornis prima*.

Unnamed Clade (*Sinovenator* + *Mei* + *Xixiasaurus* + IGM 100/44 + *Byronosaurus* + *Sinornithoides* + *Troodon* + *Saurornithoides* + *Zanabazar*)

The membership of this clade (with the exclusion of *Xixiasaurus*) is what has previously constituted Troodontidae. As such, many of the characters that optimize as synapomorphic for this clade are features previously identified as troodontid synapomorphies (Makovicky et al., 2003). In this clade a depression (possibly pneumatic) is present on the ventral surface of the postorbital process of the laterosphenoid (char. 224.1). In members of this clade, the quadrate is pneumatic (char. 299.1) and bears a single pneumatic foramen on the posteromedial surface of the corpus of the quadrate (char. 301.1). Lastly, on the pes a large longitudinal flange along the caudal or lateral face of the metatarsal IV is present (char. 229.1).

Unnamed Clade (*Mei* + *Sinovenator* + *Xixiasaurus*)

This small clade of Early Cretaceous Chinese troodontids, all from the lower part of the Yixian Formation, is supported by four unambiguous synapomorphies. Because of the fragmentary nature of *Xixiasaurus* none of four synapomorphies are known in this taxon. A single character (a maxillary process of the premaxilla that extends posteriorly to separate the maxilla from the nasal posterior to the nares: char. 20.0) unites *Xixiasaurus* with *Sinovenator* and thus places it within this clade in all the most parsimonious trees.

Sinusonasus magnodens (also from the lower Yixian Formation) is very similar to *Sinovenator changii* and likely belongs to this clade or may even be synonymous with *Sinovenator changii*. The close group relationship between *Sinovenator* and *Mei* is supported by cervical neural spines that are anteroposteriorly long (char. 99.0). Also in these taxa, the posterior

edge of ischium has a proximal median posterior process (char. 165.1).

Whereas a subarctometatarsalian pes was used to diagnosis the base of Troodontidae (Xu et al., 2002a), the subarctometatarsalian condition is now synapomorphic for this restricted troodontid clade. The condition is formed by the proximal shaft of metatarsal III being constricted and much narrower than either II or IV, but still exposed along most of the metapodium (char. 203.1). Also regarding the metapodium, *Sinovenator* and *Mei* share the presence of a mediolaterally widened metatarsal IV shaft that is flat in cross section (char. 207.1).

Unnamed Clade (IGM 100/44 + *Byronosaurus* + *Sinornithoides* + *Troodon* + *Saurornithoides* + *Zanabazar*)

A single synapomorphy supports this clade, which is the presence of a subotic recess (char. 8.1). A subotic recess is primitively absent in theropods. *Struthiomimus altus*, *Gallimimus bullatus*, *Ornithomimus edmonticus*, *Troodon formosus*, *Saurornithoides mongoliensis*, *Zanabazar junior*, *Byronosaurus jaffei*, and the Early Cretaceous troodontid IGM 100/44 possess a subotic recess. This was used by some authors (Holtz, 1998; Senter et al., 2004) to suggest a sister-group relationship between troodontids and ornithomimosaurs. It is clear that the structures in the two groups are convergent given that basal troodontids such as *Sinovenator changii, Mei long,* and two jinfengopterygine troodontids (IGM 100/1126 and IGM 100/1323) lack a subotic recess.

Unnamed Clade (*Byronosaurus* + *Sinornithoides* + *Troodon* + *Saurornithoides* + *Zanabazar*)

A single synapomorphy supports this clade. The ala parasphenoidalis is present, well developed, and crest shaped, forming the anterior edge of enlarged pneumatic recess with the ala continuous with the anterior tympanic crista (char. 468.1). This character is largely a rewording of character 6 from older TWiG matrices. The rewording reflects nomenclatural preferences as well as a slight revision to the homology concept for the character. Nevertheless, the feature it references is the enlarged pneumatic chamber associated with the inflation of the anterior tympanic recess and the full development of an ala parasphenoidalis (otosphenoidal crest of previous authors).

Unnamed Clade (*Sinornithoides* + *Troodon* + *Saurornithoides* + *Zanabazar*)

This clade is supported by maxillary and dentary teeth that lack serrations anteriorly (char. 83.1).

Unnamed Clade (*Troodon* + *Saurornithoides* + *Zanabazar*)

A slightly medially recurved symphyseal region of the dentary (char. 65.1) is an unambiguous synapomorphy for this clade. An enlarged anterior tympanic recess confluent with the subotic recess (forming the Lateral Depression sensu Currie, 1985) is an ambiguous synapomorphy for the group. This is ambiguously optimized at this node because the condition in *Sinornithoides youngi* is unknown.

Unnamed Clade (*Saurornithoides* + *Zanabazar*)

An accessory antorbital fenestra (maxillary fenestra) situated at rostral border of antorbital fossa (char. 28.0) diagnoses this clade.

Dromaeosauridae Matthew and Brown, 1922

Definition: A stem-based monophyletic group containing *Dromaeosaurus albertensis* Matthew and Brown, 1922, and all deinonychosaurs closer to it than to *Troodon formosus* Leidy, 1856, or *Passer domesticus* (Linnaeus, 1758) (sensu Sereno, 1998).

The exact set of Dromaeosauridae synapomorphies is ambiguous, because of the labile position of *Pyroraptor olympius* (fig. 59) due to the extreme paucity of data for this taxon. Considering all topologies, the

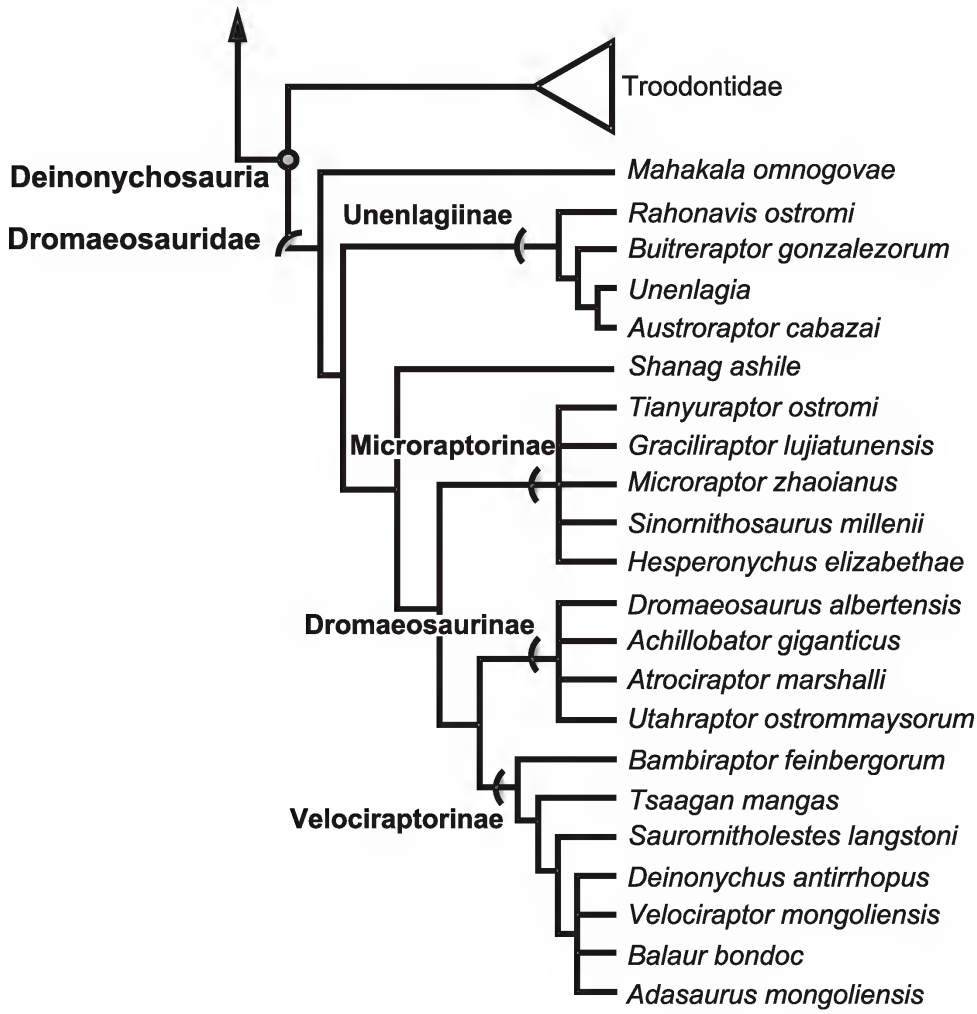


Fig. 64. Reduced strict consensus cladogram illustrating the dromaeosaurid relationships when the alternate positions of *Pyroraptor* are ignored. Troodontid taxa have been collapsed into a single terminal.

single consistent dromaeosaurid synapomorphy is the presence on the distal end of metatarsal II of a distinct and developed ginglymus (char. 201.1)—shared convergently with some avialans like *Vorona berivotrensis* UA 8651 and *Ichthyornis dispar* (Marsh, 1872, 1880; Clarke, 2004). The presence of only one synapomorphy for Dromaeosauridae occurs on the MPT where *Pyroraptor olympius* is depicted as the basalmost dromaeosaurid. When this topology is ignored (or when *Pyroraptor* is excluded from the analysis) seven additional characters are shown to be synapomorphic for the clade (fig. 64).

In alvarezsaurids (*Shuvuuia deserti* IGM 100/977 and *Mononykus olecranus* IGM 107/6) and *Archaeopteryx lithographica* BMNH 37001 there is an accessory tympanic recess located dorsal to the crista interfenestralis. This accessory recess is absent in dromaeosaurids, a condition that optimizes as a synapomorphy for the group (char. 17.0). All maniraptorans (except *Erlikosaurus andrewsi* [Clark et al., 1994], *Citipati osmolskae* IGM 100/978, and *Chirostenotes pergracilis*

[Currie and Russell, 1988]) have short paroccipital process with a convex distal end. Dromaeosaurids share a derived morphology of the paroccipital process in which it is elongate and slender, with dorsal and ventral edges nearly parallel (char. 56.0) (fig. 39). Additionally, on the paroccipital process of dromaeosaurids the dorsal edge twists anterolaterally at its distal end (char. 58.1) (fig. 39).

The teeth in dromaeosaurids lack a root-crown constriction (char. 88.1), although this is reversed to a constricted morphology in *Microraptor zhaoianus* (Hwang et al., 2002). In nearly all non-dromaeosaurid maniraptoriforms the anterior cervical centrum extends beyond the posterior limit of the neural arch. In Dromaeosauridae, the anterior cervical centrum is level with or shorter than the posterior extent of the neural arch (char. 96.0), which ultimately is a reversal of the plesiomorphic tetanuran morphology. In their detailed analysis of dromaeosaurids and, in particular, *Velociraptor mongoliensis* morphology, Norell and Makovicky (1999) showed that parapophyses on the posterior trunk vertebrae were distinctly projected on pedicels (char. 103.1) (fig. 31). This feature remains a consistent dromaeosaurid synapomorphy; however, it does occur convergently in *Mononykus olecranus* IGM 107/6, *Shuvuuia deserti* IGM 100/977 and *Confuciusornis sanctus* IVPP V11370, and in a slightly different manifestation in some ceratosaurian theropods.

A newly identified synapomorphic character from this study deals with the nature of the relatively reduced pneumaticity of the dromaeosaurid braincase (i.e., relative to most derived maniraptorans). In extant avians (Witmer, 1990), *Archaeopteryx lithographica* BMNH 37001, *Incisivosaurus gauthieri* IVPP V13326, and basal troodontids (IGM 100/1126 and IGM 100/1323) the anterior tympanic recess has migrated caudally to be located below the exit of cranial nerves VII and V. In dromaeosaurids, the lateral braincase wall is generally considered less pneumatic (Currie, 1995; Norell et al., 2006). The "basipterygoid recess" identified by Norell et al. (2006) is in fact a very anteriorly located anterior tympanic recess. Therefore, the anterior tympanic recess located anteriorly with little or no development posterior to the basipterygoid processes (char. 452.1) optimizes as a dromaeosaurid synapomorphy.

Unnamed Clade (Unenlagiinae + Microraptorinae + Dromaeosaurinae + Velociraptorinae)

Only two synapomorphies unite the four major clades of Dromaeosauridae. The two characters are the presence of pleurocoels on anterior sacrals only (char. 113.1), and a frontoparietal suture positioned well posterior to the postorbital process (char. 464.0).

Unenlagiinae Bonaparte, 1999

Definition: A stem-based monophyletic group containing *Unenlagia comahuensis* Novas and Puerta, 1997, and all coelurosaurs closer to it than to *Velociraptor mongoliensis* Osborn, 1924, *Dromaeosaurus albertensis* Matthew and Brown, 1922, *Microraptor zhaoianus* Xu et al., 2000, and *Passer domesticus* (Linnaeus, 1758) (sensu Sereno, 2005).

This clade was initially discovered and diagnosed by Makovicky et al. (2005). In this initial study, a reduced supraacetabular crest, a vertically oriented pubis, and a concave dorsocaudal edge of the ilium were synapomorphic for the group.

In the present study, the ridge bounding the cuppedicus fossa that extends far posteriorly and is confluent or almost confluent with the acetabular rim (char. 163.1) and a proximal median posterior process on the posterior edge of the ischium (char. 165.1) optimize as Unenlagiinae synapomorphies.

Also in the most parsimonious topologies the three characters found by Makovicky et al. (2005) as synapomorphic for Unenlagiinae also optimize at this node—supraacetabular crest on ilium reduced so as to not form a hood (char. 157.1), a vertically oriented pubis (char. 177.1), and a concave dorsocaudal edge of the ilium (char. 226.1). Both *Austroraptor* and *Buitreraptor* have well-defined, parallel ventrolateral ridges along the posterior cervical centra, which may turn out to be synapomorphic of the clade.

Unnamed Clade (*Buitreraptor* + *Unenlagia* + *Austroraptor*)

In both Makovicky et al. (2005) and Turner et al. (2007b) *Unenlagia* was found as the sister taxon to *Rahonavis ostromi* to the exclusion of *Buitreraptor gonzalezorum*. In the present analysis, this topology was not recovered. Five synapomorphies unite *Buitreraptor gonzalezorum*, *Austroraptor cabazai*, and *Unenlagia*. These include a metatarsal III with a constricted proximal shaft that is much narrower than either metatarsals II or IV, but still exposed along most of metapodium—the so-called subarctometatarsal condition (char. 203.1), a large longitudinal flange along the caudal or lateral face of metatarsal IV (char. 229.1), the presence of a postacetabular end of the ilium with a lobate brevis shelf projecting from the ilium beyond the end of postacetabular lamina (char. 227.1), thoracic vertebral centra with a length markedly greater than midpoint width (char. 317.0), and a convex scapular articular surface on the coracoid (char. 339.1).

The subarctometatarsalian condition is present in a number of other paravians including most microraptorines and the troodontids *Mei long*, *Sinovenator changii*, and *Sinornithoides youngi*. A lobate brevis shelf is present convergently in *Microraptor zhaoianus* (Hwang et al., 2002). This feature is not present in *Rahonavis ostromi* (UA 8656), which instead exhibits an ilium with a rounded posterior margin in dorsal view. A convex scapular articular surface on the coracoid is a feature seen in derived enantiornithines, but is also present in these two unenlagiine taxa. *Rahonavis ostromi* (UA 8656) lacks a coracoid, but the coracoid facet on the scapula is flat to weakly concave, suggesting the potential for an intermediate morphology in the sister taxon to *Buitreraptor* + *Unenlagia*.

Unnamed Clade (*Unenlagia* + *Austroraptor*)

Austroraptor cabazai is found here as the sister taxon of *Unenlagia*. This position is consistent with the results of Novas et al. (2009), as they found an unresolved clade containing *Unenlagia*, *Austroraptor*, and *Rahonavis*. Our analysis departs from the results of Novas et al (2009) in that we find *Buitreraptor gonzalezorum* as the sister taxon to *Unenlagia* + *Austroraptor*, with *Rahonavis* being the basalmost unenlagiine dromaeosaurid. Three characters support the sister-group status of *Unenlagia* and *Austroraptor*. These synapomorphies are neural spines on the dorsal vertebrae that expand to form a spine table (char. 108.1), a calcaneum and astragalus that are unfused to each other or to the tibia (char. 198.0), and the presence of pleurocoels in the dorsal vertebrae (char. 265.1/2).

Unnamed Clade (*Shanag* + Microraptorinae + Velociraptorinae + Dromaeosaurinae)

Two characters unite the small Asian dromaeosaurids *Shanag ashile* with dromaeosaurids more derived than unenlagiines. These are maxillary and dentary teeth that lack serrations anteriorly (char. 83.1) and the dorsal displacement of the accessory antorbital (maxillary) fenestra (char. 237.1).

Unnamed Clade (Microraptorinae + Velociraptorinae + Dromaeosaurinae)

Two characters unite microraptorine, velociraptorine, and dromaeosaurine taxa. Members of this clade possess a tertiary antorbital fenestra (promaxillary fenestra) (char. 29.1) and the nutrient foramina are superficial on the external surface of dentary (char. 71.1).

Microraptorinae Senter et al., 2004

Definition: A stem-based monophyletic group containing *Microraptor zhaoianus* Xu et al., 2000, and all coelurosaurs closer to it than to *Dromaeosaurus albertensis* Matthew and Brown, 1922, *Velociraptor mongoliensis* Osborn, 1924, *Unenlagia comahuensis* Novas and Puerta, 1997, and *Passer domesticus* (Linnaeus, 1758) (sensu Sereno, 2005).

Five synapomorphies unite *Tianyuraptor*, *Microraptor*, *Graciliraptor*, *Hesperonychus*, and *Sinornithosaurus* in Microraptorinae. These are a semilunate distal carpal that is small and covers about half the base of metacarpals I and II (char. 148.1), a proximal shaft of metatarsal III that is constricted and much narrower than either metatarsal II

or IV, but still exposed along most of the metapodium (subarctometatarsal: char. 203.1), the lateral face of pubic shaft possesses a prominent lateral tubercle about halfway down the shaft (char. 231.1), the caudal chevrons have very elongated posterior extensions (char. 442.1), and the combined length of metacarpal I plus phalanx I-1 is equal to or less than the length of metacarpal II (char. 444.1).

Eudromaeosauria (i.e., Velociraptorinae + Dromaeosaurine) Longrich and Currie, 2009

Definition: The node-based monophyletic group containing the last common ancestor of *Saurornitholestes langstoni* Sues, 1978, *Deinonychus antirrhopus* Ostrom, 1969, *Dromaeosaurus albertensis* Matthew and Brown, 1922, and *Velociraptor mongoliensis* Osborn, 1924, and all its descendants.

Like many of the other larger clades within Dromaeosauridae, the many alternate positions of *Pyroraptor olympius* result in ambiguous character optimizations. For the clade composed of Velociraptorinae and Dromaeosaurinae only one character optimizes at this node in all trees. The apomorphic character is a flexor heel on phalanx II-2 that is long and lobate, with an extension of the midline ridge onto the dorsal surface of the heel (char. 228.1). More basally positioned dromaeosaurids display a small and typically asymmetrically developed heel present primarily on the medial side of the vertical ridge on the proximal articulation surface.

When *Pyroraptor olympius* is not the sister taxon to this clade then eight additional characters are found to be synapomorphies. This includes a maxillary process of the premaxilla that extends posteriorly to separate the maxilla from the nasal posterior to nares (char. 20.2)—a feature otherwise only seen in ornithomimosaurs. Two characteristics of the frontal diagnose this clade of dromaeosaurids: the postorbital process of the frontal is sharply demarcated from the orbital margin (char. 43.1—a trait discussed by Currie, 1995); and the frontal edge is notched in the region of the lacrimal suture (char. 44.1). In this clade the internal mandibular fenestra is large and rounded (char. 73.1). Typically in coelurosaurs the internal mandibular fenestra is small and slitlike. Apart from this clade of dromaeosaurids, only some tyrannosaurids (e.g., *Tyrannosaurus rex* FMNH PR 2081) and *Incisivosaurus gauthieri* (IVPP V13326) have a large and rounded internal mandibular fenestra. On the lateral braincase wall of velociraptorines and dromaeosaurines, a shallow prootic recess is present (char. 450.1). This optimizes as a synapomorphy for the clade because it is observable in *Dromaeosaurus albertensis* (AMNH FARB 5356), *Bambiraptor feinbergorum* (AMNH FARB 30556), and *Tsaagan mangas* (IGM 100/1015). Among other members of Dromaeosaurinae and Velociraptorinae the presence of this morphology is unknown. Among more basal dromaeosaurids, only *Microraptor zhaoianus* (IVPP V uncataloged 3) is known to lack a prootic recess, so it is possible that this feature has a broader distribution within Dromaeosauridae, but the plesiomorphic lack of a prootic recess in basal dromaeosaurids is entirely consistent with the absence of this recess in all troodontids and avialans with known and observable braincase material (e.g., IGM 100/1126 and *Archaeopteryx lithographica* BMNH 37001, respectively).

Two vertebral synapomorphies characterize this clade: no carotid processes on the posterior cervical vertebrae (char. 97.0) and thoracic vertebral centra with lengths markedly greater than midpoint widths (char. 317.0). Additionally, the acromion process of the scapula does not project anteriorly past the articular surface for the coracoid (char. 354.1).

Dromaeosaurinae Matthew and Brown, 1922

Definition: A stem-based monophyletic group containing *Dromaeosaurus albertensis* Matthew and Brown, 1922, and all coelurosaurs closer to it than to *Velociraptor mongoliensis* Osborn, 1924, *Microraptor zhaoianus* Xu et al., 2000, *Unenlagia comahuensis* Novas and Puerta, 1997, and *Passer domesticus* (Linnaeus, 1758) (sensu Sereno, 2005).

Dromaeosaurinae was diagnosed by Currie (1995) as identical to *Dromaeosaurus albertensis* because at the time he considered it the only clear member of Dromaeosaurinae (although he considered *Adasaurus mongoliensis* as a potential member). Currie's (2005) diagnosis included an anterior carina of maxillary or mandibular teeth that twist toward the lingual surface.

Because early phylogenetic analyses of coelurosaur relationships considered Dromaeosauridae at a supraspecific level (Sereno, 1997, 1999; Holtz, 1998), interrelationships among dromaeosaurids were not considered, and so content of and/or monophyly of the Dromaeosaurinae/Velociraptorinae dichotomy were not tested. Early analyses utilizing the versions of the TWiG matrix recovered little or no consensus on dromaeosaurid interrelationships (e.g., Norell et al., 2001; Hwang et al., 2002; Makovicky et al., 2003) (fig. 3). Later analyses revealed that underlying structure existed within Dromaeosauridae by increasing character sampling (Makovicky et al., 2005) or looking at reduced strict and Adams consensuses (Novas and Pol, 2005; Norell et al., 2006; Turner et al., 2007a). These analyses showed that distinct Dromaeosaurinae and Velociraptorinae clades exist. In these analyses Dromaeosaurinae consisted of *Dromaeosaurus albertensis*, *Utahraptor ostrommaysorum*, *Achillobator giganticus*, and *Adasaurus mongoliensis* with *Saurornitholestes langstoni* variably resolving as a member of this group.

Our study identifies four unambiguous synapomorphies for Dromaeosaurinae. These include maxillary and dentary teeth with serrations on both anterior and posterior margins (char. 83.0)—a particularly homoplastic character when considered across all coelurosaur diversity, but one that provides strong support for lower level clades. The pubis in dromaeosaurines is vertically oriented (char. 177.1) and the pubic boot projects anteriorly and posteriorly (char. 178.0). In the skull, the jugal process of the maxilla, ventral to the external antorbital fenestra, is dorsoventrally wide (char. 238.1). The twisting carinae noted by Currie (1995) remain an autapomorphy for *Dromaeosaurus albertensis* and is not indicative of a more inclusive clade.

Dromaeosaurus albertensis, *Utahraptor ostrommaysorum*, *Achillobator giganticus* and the poorly known *Atrociraptor marshalli* are the only dromaeosaurine taxa in the present study. Firsthand reexamination of *Adasaurus mongoliensis* resulted in 102 changes to the character scoring of taxon (table 3), which resulted in the repositioning of it as a velociraptorine and, further, in the clarification of the position of *Saurornitholestes langstoni*.

Velociraptorinae Barsbold, 1983

Definition: A stem-based monophyletic group containing *Velociraptor mongoliensis* Osborn, 1924, and all coelurosaurs closer to it than to *Dromaeosaurus albertensis* Matthew and Brown, 1922, *Microraptor zhaoianus* Xu et al., 2000, *Unenlagia comahuensis* Novas and Puerta, 1997, and *Passer domesticus* (Linnaeus, 1758) (sensu Sereno, 2005).

Velociraptorinae was diagnosed by Currie (1995) as dromaeosaurids with maxillary and dentary teeth possessing denticles on the anterior carinae that are significantly smaller than the posterior denticles, and which have a second premaxillary tooth that is significantly larger than the third and fourth premaxillary teeth. Currie (1995) also considered nasals that are depressed in lateral view (an observation strongly supported by Paul, 1988) as diagnostic for velociraptorines although he did note that that element was unknown in *Dromaeosaurus,* so the character was equivocally diagnostic of dromaeosaurids he considered Velociraptorinae (*Deinonychus antirrhopus*, *Saurornitholestes langstoni*, *Velociraptor mongoliensis*, and *Utahraptor ostrommaysorum*).

Similar to Dromaeosaurinae, cladistic tests of Velociraptorinae monophyly did not happen until the first species-level phylogenies were made (e.g., Norell et al., 2001) and, as was the case with Dromaeosaurinae, these early analyses found little consensus on interrelationships among dromaeosaurids. The reduced strict consensus of Novas and Pol (2005) recovered a distinct velociraptorine clade, which included *Velociraptor mongoliensis*, *Deinonychus antirrhopus*, and *Tsaagan mangas* (unnamed at the time). The position of *Saurornitholestes* was labile and therefore unclear whether it belonged to

Velociraptorinae. Similar resolution and membership was found by Makovicky et al. (2005), Norell et al. (2006), and Turner et al. (2007a, 2007b). Neither Senter et al. (2004) nor Senter (2007) recovered a Velociraptorinae clade. In his most recent analysis (Senter, 2007), *Deinonychus antirrhopus*, *Saurornitholestes langstoni*, *Velociraptor mongoliensis*, *Adasaurus mongoliensis*, and *Tsaagan mangas* (labeled IGM 100/1015) were found as successive sister taxa to a Dromaeosaurinae clade identical in composition to that recovered in our study.

The phylogenetic analysis from our study recovers a monophyletic and well-supported Velociraptorinae clade composed of *Bambiraptor feinbergorum*, *Tsaagan mangas*, *Saurornitholestes langstoni*, *Deinonychus antirrhopus*, *Velociraptor mongoliensis*, and *Adasaurus mongoliensis*. The character-scoring changes for *Adasaurus mongoliensis* resulted in repositioning of it as a derived velociraptorine as opposed to the dromaeosaurine position recovered in previous analyses (e.g., Turner et al., 2007a, 2007b).

This clade is supported by three unambiguous synapomorphies. The posterior opening of the basisphenoid recess is divided into two small, circular foramina by a thin bar of bone (char. 10.1), and the dorsal tympanic recess is present as a deep, posterolaterally directed concavity (char. 16.2). Pleurocoels are present in all dorsal vertebrae (char. 265.2). An additional feature, an accessory depression in the supratemporal fossa (char. 466.1), may serve as a future synapomorphy for this clade. Due to the unknown presence or absence of this feature in *Shanag*, it is currently optimized as an ambiguous synapomorphy for the group.

Unnamed Clade (*Tsaagan* + *Saurornitholestes* + *Deinonychus* + *Velociraptor* + *Adasaurus* + *Balaur*)

A single synapomorphy supports this group of velociraptorine dromaeosaurids. Exits of cranial nerves X–XII that are located together in a bowllike depression (char. 19.1) optimizes as synapomorphic for this clade, however, this character is preserved only in *Tsaagan mangas* and *Velociraptor mongoliensis*.

Unnamed Clade (*Saurornitholestes* + *Deinonychus* + *Velociraptor* + *Adasaurus* + *Balaur*)

This clade is supported by the presence of a dorsal recess on the ectopterygoid (char. 60.1)—unknown in *Adasaurus mongoliensis* and paralleled in *Archaeopteryx lithographica*. Additionally, the first premaxillary tooth in these taxa (unknown in *Adasaurus mongoliensis*) are much smaller than crowns of premaxillary teeth 2 and 3 (char. 251.1).

Unnamed Clade (*Deinonychus* + *Velociraptor* + *Adasaurus* + *Balaur*)

This clade is supported by a single feature—the shaft of metatarsal IV mediolaterally wide and flat in cross section (char. 207.1). This trait is paralleled in *Utahraptor ostrommaysorum* and the troodontid clade of *Mei* + *Sinovenator*.

The uncertain position of *Balaur* within this clade collapses resolution within the group. When *Balaur* is excluded from the analysis an additional synapomorphy unites *Deinonychus*, *Velociraptor*, and *Adasaurus*. Basal dromaeosaurids like *Sinornithosaurus millenii*, *Microraptor zhaoianus*, *Rahonavis ostromi*, *Buitreraptor gonzalezorum*, basal velociraptorines, and avialans possess scapulae that are shorter than the humerus. Because of missing data in *Mahakala omnogovae*, *Pyroraptor olympius*, and dromaeosaurines, and because of the long scapulae of troodontids, the ancestral morphology for Dromaeosauridae, Deinonychosauria, and Paraves is ambiguous. However, because of the short scapula relative to humeral length in basal dromaeosaurids, the reversal to a long scapula relative to the humerus (char. 139.0) is optimized as a synapomorphy for the *Deinonychus* + *Velociraptor* + *Adasaurus* clade.

Likewise in the absence of *Balaur*, *Velociraptor* and *Adasaurus* are united as sister taxa. A fused scapulocoracoid (char. 135.1), a calcaneum and astragalus fused to each other but not to the tibia (char. 198.1), and distal tarsals fused to metatarsals (char. 199.1) support the monophyly of these two taxa. Because all the synapomorphies of this clade relate to increased fusion of skeletal

elements, the shared similarity between them could reflect ontogenetic variability. Clarifying whether these synapomorphies reflect common descent or senescene will require additional work assessing the ontogenetic stage of the specimens for these taxa as well as additional specimens of *Adasaurus*.

Avialae Gauthier, 1986

Definition: A stem-based monophyletic group containing *Passer domesticus* (Linnaeus, 1758) and all coelurosaurs closer to it than to *Dromaeosaurus albertensis* Matthew and Brown, 1922, or *Troodon formosus* Leidy, 1856 (sensu Maryanska et al., 2002).

Sixteen unambiguous synapomorphies support the monophyly of Avialae (fig. 65). Some of these synapomorphic characters relate to modifications of the skull associated with increased pneumaticity as well as more extensive coossification. A number of the characters are associated with flight-related morphology such as forelimb elongation, hindlimb reduction, tail reduction, and modifications to the pelvis likely associated with restructuring of the hip and femoral musculature. These characters are: asymmetric vaned feathers on forelimb (char. 1.1); caudal (posterior) tympanic recess extends into opisthotic posterodorsal to fenestra ovalis, confluent with this fenestra (char. 18.2); parietals separate (char. 46.0); lateral border of quadrate shaft straight (char. 53.0); preacetabular portion of ilium markedly longer (more than 2/3 of total ilium length) than postacetabular part (char. 155.1); posterior edge of ischium with proximal median posterior process (char. 165.1); pubic apron less than 1/3 of shaft length (char. 181.1); metatarsal I articulates with the medial surface of metatarsal II at the distal end (char. 205.3); ulna/femoral length ratio equal to or greater than one (char. 236.1); in lateral view, dorsal border of the antorbital fossa formed by the lacrimal and nasal (char. 243.1); ratio of femur to humerus less than 1 (char. 266.2); basisphenoid/pterygoid articulation oriented mediolaterally (char. 283.1); pterygoid, articular surface for basisphenoid flat to convex (char. 284.1); thoracic vertebral centra approximately equal in length and midpoint width (char. 317.0); distalmost mediolateral width of tibia approximately equal to shaft width, no distal expansion of whole shaft, although condyles may be variably splayed mediolaterally (char. 426.1); combined length of metacarpal I plus phalanx I-1 equal to or less than length of metacarpal II (char. 444.1).

Unnamed Clade (*Sapeornis* + *Jeholornis* + *Jixiangornis* + Pygostylia)

This clade of avialans is extremely well supported (GC = 89) with little conflicting data and Bremer support of 2. Thirteen unambiguous synapomorphies support its monophyly. The dorsal surfaces of the parietals are flat and a lateral ridge borders the supratemporal fenestra (char. 45.0), although this character reverses apomorphically in Euornithes to dorsally convex with a very low sagittal crest. This node also marks the beginning of increased sacralization of vertebrae (6 to 7 sacral vertebrae: char. 110.1/2). In these taxa, the prezygapophyses of distal caudal vertebrae are between 1/3 and whole centrum length (char. 120.0), and the obturator process of the ischium is absent (char. 169.0).

At this level of the tree, the fibula is short and not in contact with the proximal tarsals (char. 191.1), the distal end of astragalus and calcaneum form distinct condyles separated by a prominent tendoneal groove on the anterior surface (char. 194.1), and the distal tarsals fuse to the metatarsals forming a tarsometatarsus (char. 199.1). The proximodorsal process of the ischium (when present in the basal taxa) is large, proximodorsally hooked and separated from the iliac peduncle of the ischium by a notch (char. 230.1). Pleurocoels are present in all dorsals (char. 265.2) and the lateral surfaces of thoracic vertebral centra bear deeply emarginated fossae (char. 318.1).

The ulna and humerus are approximately equal in length (char. 356.1) although *Confuciusornis sanctus* IVPP V11374, *Patagopteryx deferrariisi* MACN N 11, *Hongshanornis longicresta* IVPP V14533, *Hesperornis regalis* (Marsh, 1880), *Baptornis advenus* (Marsh, 1877a), and *Anas platyrhynchus* (AMNH 27496) reverse to the condition of having a humerus longer than the ulna. The semilunate carpal and metacarpals exhibit incomplete proximal fusion (char. 390.1) and

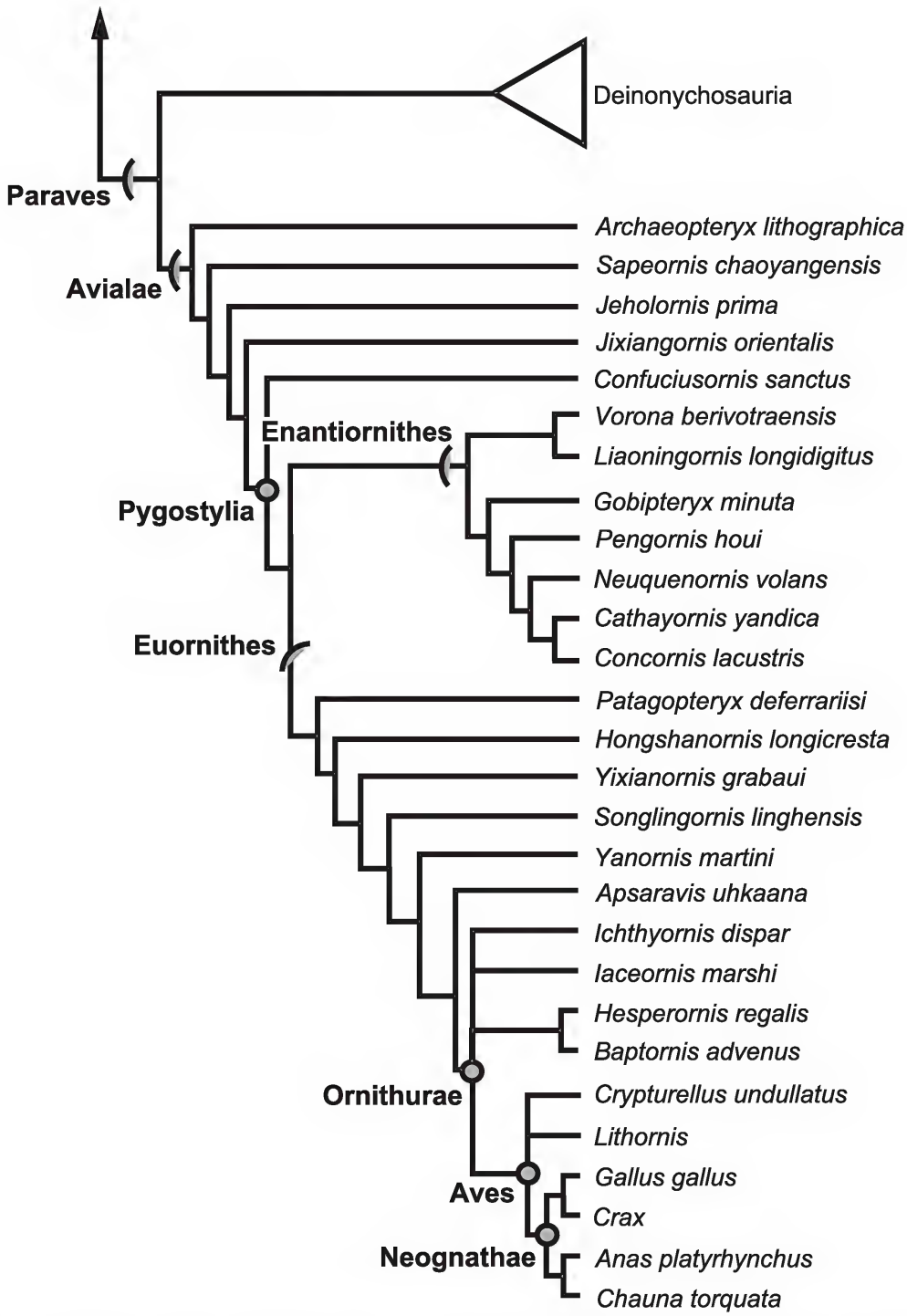


Fig. 65. Reduced strict consensus cladogram illustrating avialan relationships when the alternate positions of *Limenavis* are ignored. Deinonychosaurian taxa have been collapsed into a single terminal.

metatarsal I is curved or distally deflected, but not twisted with the ventral surface convex and J-shaped (char. 432.1).

Unnamed Clade (*Jeholornis* + *Jixiangornis* + Pygostylia)

Like the previous node, this node is extremely well supported with 11 synapomorphies and few conflicting topologies in the jackknife analysis (GC = 84). Many of the synapomorphies for this clade mark the first occurrence of very "avian"-like characteristics. For example, it is at this node that both an edentulous premaxilla (char. 80.1) and maxilla (char. 82.1) evolved and the nasal (frontal) process of premaxilla becomes long and closely approaches the frontal (char. 273.1).

The shoulder girdle also begins to take on a more modern aspect with the coracoids possessing a strutlike morphology (in lateral view the coracoid is more than twice as tall as wide: char. 136.3). The scapula and coracoid articulation takes on a "ball and socket" conformation with a pit-shaped scapular cotyla developed on the coracoid and coracoidal tubercle developed on the scapula (char. 339.0). The glenoid facet of the coracoid migrates ventral to the acrocoracoid process (char. 347.1). The angle between the coracoid and scapula at the glenoid is 90° or less (char. 351.1) and the posterior end of the scapula tapers distally (char. 352.1).

The arm and the metatarsus also assume a more "modern" aspect. The distal articular surface of the ulna (dorsal condyle and dorsal trochlea in birds) becomes a convex semilunate surface (char. 143.1) and metacarpal III is bowed (char. 445.1). In the metatarsus, coossification of metatarsals begins proximally (char. 200.1).

Unnamed Clade (*Jixiangornis* + Pygostylia)

The sister-group relationship of *Jixiangornis* to Pygostylia has high jackknife support and moderate Bremer support. Five unambiguous morphological changes are synapomorphic for this node. The sacral vertebrae in these taxa have unfused zygapophyses (char. 111.0) and the ossified uncinate processes remain unfused to the ribs (char. 125.1). It is at this level of the paravian tree that the ossified sternal plates fuse to each other (char. 128.1). Members of this clade have thoracic vertebrae with centra markedly longer than midpoint width (char. 317.1), although two apparently independent reversals to more boxlike thoracic vertebrae occur in *Patagopteryx deferrariisi* and *Hongshanornis longicresta*. The dorsal process of the ischium contacts the ilium (char. 404.1) in basal members of this clade (e.g., *Jixiangornis orientalis*, *Confuciusornis sanctus*, *Cathayornis yandica*), but a reversal to the plesiomorphic noncontacting relationship occurs in Euornithes. Metatarsal V is absent (char. 427.1) in *Jixiangornis orientalis* and all more derived avialans; however, retention of the metatarsal in *Confuciusornis* and *Vorona* makes the optimization of this character state at this node ambiguous.

Pygostylia Chatterjee, 1997

Definition: A node-based monophyletic group including the last common ancestor of *Confuciusornis sanctus* Hou et al., 1995, and *Passer domesticus* (Linnaeus, 1758) and all of its descendants (sensu Chiappe, 2001).

Expectedly, an abbreviated tail with less than eight free caudal vertebrae (char. 121.3) and distal caudals that are fused into a pygostyle (char. 323.1), optimize as synapomorphic for this node. The pubic boot is absent in pygostylians with no anteroposterior projections (char. 178.2) except for *Cathayornis yandica*, which shows a reversal to the condition of a slightly posteriorly projecting pubic boot.

In the skull, the dentary is subtriangular in lateral view (char. 70.0), symphyseal foramina are present at the mandibular symphysis (char. 306.1)—a feature completely unique among coelurosaurs, and the Meckelian groove is covered by the splenial and is not exposed medially (char. 309.1). The proximoposterior surface of the deltopectoral crest of the humerus is concave (char. 365.1) and the distal condyles of the humerus are developed on the anterior surface of the humerus (char. 371.1).

It is at this node within Avialae that the pelvis shows signs of increased fusion (i.e., the ilium, ischium, and pubis are partially fused proximally: char. 402.1). On the hindlimb, a laterally projected fibular trochlea developed as a small notch (char. 418.1) is present,

although this character shows further transformation into a shelflike conformation in ornithurines. Distally on the tibia, the articular surface for the distal tarsals/tarsometatarsus is well developed posteriorly forming the sulcus cartilaginis tibialis of Aves (Baumel and Witmer, 1993) and a distinct articular surface that extends up the posterior surface of the tibiotarsus (char. 425.1) is present. Lastly, a proximal vascular foramen on the tarsometatarsus is present as a single foramen between metatarsals III and IV (char. 431.1).

Ornithothoraces (i.e., Enantiornithes + Euornithes) Chiappe and Calvo, 1994

Definition: The node-based monophyletic group containing the last common ancestor of *Iberomesornis romerali* Sanz and Bonaparte, 1992, and *Passer domesticus* (Linnaeus, 1758) and all of its descendents (sensu Chiappe, 1995).

Eight unambiguous synapomorphies support the monophyly of this clade. Ornithothoracines have nutrient foramina on the external surface of dentary that lie within a deep groove (char. 71.1). The posterior margin of the sternum has distinct posteriorly projected medial and/or lateral processes (char. 333.1) and the interclavicular angle of the furcula is less than 90° (char. 335.1).

A number of changes on the humerus and wrist optimize here and are further modified toward what can be considered a modern avian morphology. These include a ventral tubercle and capital incisure present on the proximal part of the humeral head (char. 359.1), a transverse groove present and developed as a discreet, depressed scar on the proximal surface of the bicipital crest or as a slight transverse groove (char. 362.1), the semilunate carpal and metacarpal exhibiting complete proximal fusion (char. 390.2), and the presence of a pisiform process (char. 394.1). At the ankle, the tibiotarsus-formed condyles are equal in anterior projection (char. 419.1) as opposed to the plesiomorphic condition where the medial condyle typically projects further anteriorly.

Enantiornithes Walker, 1981

Definition: A stem-based monophyletic group containing *Cathayornis yandica* Zhou et al., 1992, and all coelurosaurs closer to it *Passer domesticus* (Linnaeus, 1758) (sensu Sereno, 2005).

Only two synapomorphies support the monophyly of Enantiornithes with *Liaoningornis* and *Vorona* as the basalmost members. These features are a toothed premaxilla (char. 80.0) and a toothed maxilla (char. 82.0).

Euornithes Cope, 1889

Definition: A stem-based monophyletic group containing *Passer domesticus* (Linnaeus, 1758) and all coelurosaurs closer to it than to *Cathayornis yandica* Zhou et al., 1992 (sensu Sereno, 1998).

Euornithes is a strongly supported clade in our analysis. The dorsal surfaces of the parietals are dorsally convex with a low sagittal crest along the midline (char. 45.1). The metatarsals show increased fusion relative to outgroups with metatarsals fusing to each other proximally and distally (char. 200.3). Metatarsal I articulates on the posterior surface of the distal quarter of metatarsal II (char. 205.1). The scapula in euornithines is dorsoventrally curved (char. 353.1). The ilium, ischium, and pubis show complete fusion proximally (char. 402.2) and the dorsal process of the ischium fails to contact the ilium (char. 404.0). The posterior trochanter, present ancestrally in paravians, is lost on the femur (char. 414.2) within Euornithes. On the tarsometatarsus, a characteristically "avian" feature—the hypotarsus—first arises in this clade. The hypotarsus is a structure associated with the passage of tendons of the pedal flexors in living birds. In Euornithes the hypotarsus takes the form of a projected surface or grooves on the proximoposterior surface developed as a posterior projection with a flat posterior surface (char. 430.1).

Unnamed Clade (*Hongshanornis* + *Yixianornis* + *Songlingornis* + *Yanornis* + *Apsaravis* + Ornithurae)

This clade of euornithines has moderate to low support. Four synapomorphies unite these taxa. In this clade, the procoracoid

process is present on the coracoid (char. 340.1) and the proximal end of the humeral head is domed proximally (char. 357.1). In the manus, phalanx 1 of digit II is strongly dorsoventrally compressed with a flat caudal surface (char. 399.1). Lastly, at the ankle the condyles of the tibiotarsus are approximately equal in mediolateral width (char. 422.1) as opposed to the plesiomorphic condition where the medial condyle is wider.

Unnamed Clade (*Yixianornis* + *Songlingornis* + *Yanornis* + *Apsaravis* + Ornithurae)

Eight unambiguous synapomorphies support this clade. These include a dentary with subparallel dorsal and ventral edges (char. 70.1) and a toothed premaxilla (char. 80.1). In the pelvis, a preacetabular part of the ilium that is roughly as long as the postacetabular part of the ilium (char. 155.0) and an anterior end of the ilium that is gently rounded or straight (char. 156.0) unite these taxa.

Additional synapomorphies include a lateral process on the coracoid (char. 345.1), a medially hooked acrocoracoid (char. 349.1), an anteroposterior diameter of metacarpal III that is approximately equal to or greater than 50% of the anteroposterior diameter of metacarpal II (char. 391.1), and a metatarsal III that is proximally displaced plantarly relative to metatarsals II and IV (char. 428.1).

Unnamed Clade (*Songlingornis* + *Yanornis* + *Apsaravis* + Ornithurae)

Recent analysis examining basal euornithine relationships have typically recovered a *Yixianornis* + *Songlingornis* + *Yanornis* clade. The clade was not recovered in our analysis. Instead, two unambiguous synapomorphies united *Songlingornis* and *Yanornis* with more derived avialans—a fully toothed maxilla (char. 82.0) and dentary (char. 220.0). These are very homoplastic characters in this part of the tree. As such, this should not be considered a strong contradiction of the possible *Yixianornis* + *Songlingornis* + *Yanornis* clade.

Unnamed Clade (*Yanornis* + *Apsaravis* + Ornithurae)

A single synapomorphy unites *Yanornis* with *Apsaravis* and Ornithurae. The presence of small but numerous (25–30) teeth in the maxilla and dentary (char. 84.1) optimizes at this node.

Unnamed Clade (*Apsaravis* + Ornithurae)

This clade is diagnosed by possessing cervical and anterior trunk vertebrae that are at least partially heterocoelous (char. 101.2), the presence of 10 or more sacral vertebrae (char. 110.5), distal articular end of metacarpal II that is ginglymoid and a metacarpal I that is shelflike (char. 213.2), and pubes that are compressed mediolaterally (char. 412.1), and do not contact each other distally (char. 413.1). The tarsometatarsus within members of this clade bears a distinct, well-developed, and globose intercotylar eminence (char. 429.1) and metatarsal I is absent (char. 447.1).

Ornithurae Haeckel, 1866

Definition: A node-based monophyletic group including the last common ancestor of *Hesperornis regalis* Marsh, 1880, and *Passer domesticus* (Linnaeus, 1758) and all of its descendents (sensu Chiappe, 1995).

Eight synapomorphies diagnose this clade of derived avialans with a Recent avian aspect (although *Hesperornis* and *Ichthyornis* still retain teeth). In these taxa, the anterior trunk vertebrae have large hypapophyses (char. 102.1) and the acromion margin of the scapula is laterally everted (char. 133.1). On the humerus, a brachial fossa is present and developed as a flat scar or as a scarred fossa (char. 376.1) and demarcation of muscle origins (e.g., m. extensor metacarpi radialis in Aves) on the dorsal edge of the distal humerus are present as pit-shaped scars or as variably projected scar-bearing tubercles or facets (char. 378.1). The ulnare in ornithurines is V-shaped with well-developed dorsal and ventral rami (char. 388.1) and the tibiotarsal condyles bear an extensor canal present as an emarginated groove (char. 420.1). There are two proximal vascular foramina on the

tarsometatarsus (char. 431.2) and the distal plantar surface of metatarsal II possesses a fossa (in the form of a shallow notch) for metatarsal I (char. 433.1).

Aves Linnaeus, 1758

Definition: A node-based monophyletic group containing the last common ancestor of *Struthio camelus* (Linnaeus, 1758), *Tinamus major* (Gmelin 1789), and *Passer domesticus* (Linnaeus, 1758) and all of its descendents (sensu Gauthier, 1986, and Gauthier and de Queiroz, 2001).

Due to the lability of some taxa closely related to Aves (e.g., *Limenavis patagonicus*, and *Iaceornis marshi*) the characters diagnosing Aves vary among topologies. In a reduced taxon-sampling analysis, a subset of these potential synapomorphies stabilize and that set is used here for the purposes of diagnosing this clade. Nineteen unambiguous synapomorphies diagnose Aves. This will be listed below but not discussed further: supraorbital crests on lacrimal with lateral expansion anterior and dorsal to orbit (char. 37.2); dorsal surface of parietals flat, lateral ridge borders supratemporal fenestra (char. 45.0); maxilla edentulous (char. 82.1); 11 or more sacral vertebrae (char. 110.6/7); obturator process of ischium proximal in position (char. 169.1); dentary edentulous (char. 220.2); in lateral view no dorsal projection of maxilla participates in the anterior margin of the internal antorbital fenestra (char. 241.2); dentaries fused anteriorly (char. 270.1); maxillary process of the premaxilla extending for at least half the length of the facial margin (char. 272.1); kinked pterygoid absent, basipterygoid articulation in line with axis of pterygoid (char. 285.1); mandibular articulation of quadrate tricondylar due to presence of additional posterior condyle or broad articular surface (char. 298.1); sternal pneumatic foramina present in the depressions (loculi costalis; Baumel and Witmer, 1993) between rib articulations (char. 329.1); paired intermuscular ridges (linea intermuscularis; Baumel and Witmer, 1993) parallel to the sternal midline (char. 332.1); a pneumatized coracoid (char. 343.1); proximal end of the humerus with one or more pneumatic foramina (char. 370.1); preacetabular blade of the ilium extending anterior to the first sacral vertebrae and overlapping one or more ribs (char. 408.1); medial condyle of the tibiotarsus that projects further anteriorly than laterally (char. 419.0); projected surface or grooves on proximoposterior surface of tarsometatarsus (associated with the passage of tendons of the pes flexors in Aves; hypotarsus) (char. 430.2); distal vascular foramen forked, two exits (plantar and distal) between metatarsals III and IV (char. 436.1).

Nodal Support

Character support for the nodes present in the most parsimonious reconstructions was calculated using two methods. The first is a statistical resampling technique, the jackknife applied to character resampling (Farris et al., 1996). Farris et al. and others (e.g., Goloboff et al., 2003) have given detailed reasons for preferring this measure over the more commonly employed nonparametric bootstrap resampling (Felsenstein, 1985), which relies on assumptions not met by our dataset (or most other morphological datasets). The second method used is Bremer support (Bremer, 1988, 1994), which evaluates node stability/sensitivity by exploring suboptimal tree solutions in order to determine how many additional steps must be allowed in searching for topologies before the hypothesized clade is no longer recovered. Bremer support was calculated using negative constraints through the use of the BREMER.RUN script supplied with TNT.

The jackknife support analysis was calculated using TNT (Goloboff et al., 2008a, 2008b). The analysis was performed using 1000 replicates for which the probability of independent character removal was set to 0.20. Each jackknife replicate was analyzed using a tree search strategy consisting of 10 replicates of RAS followed by TBR branch swapping (saving 10 trees per replicate). The topologies obtained during the jackknife replicates are summarized using GC frequencies. This follows the recommendations of Goloboff et al. (2008a, 2008b). These frequencies differ from the raw clade frequencies, because they measure the difference in frequency between the analyzed group and

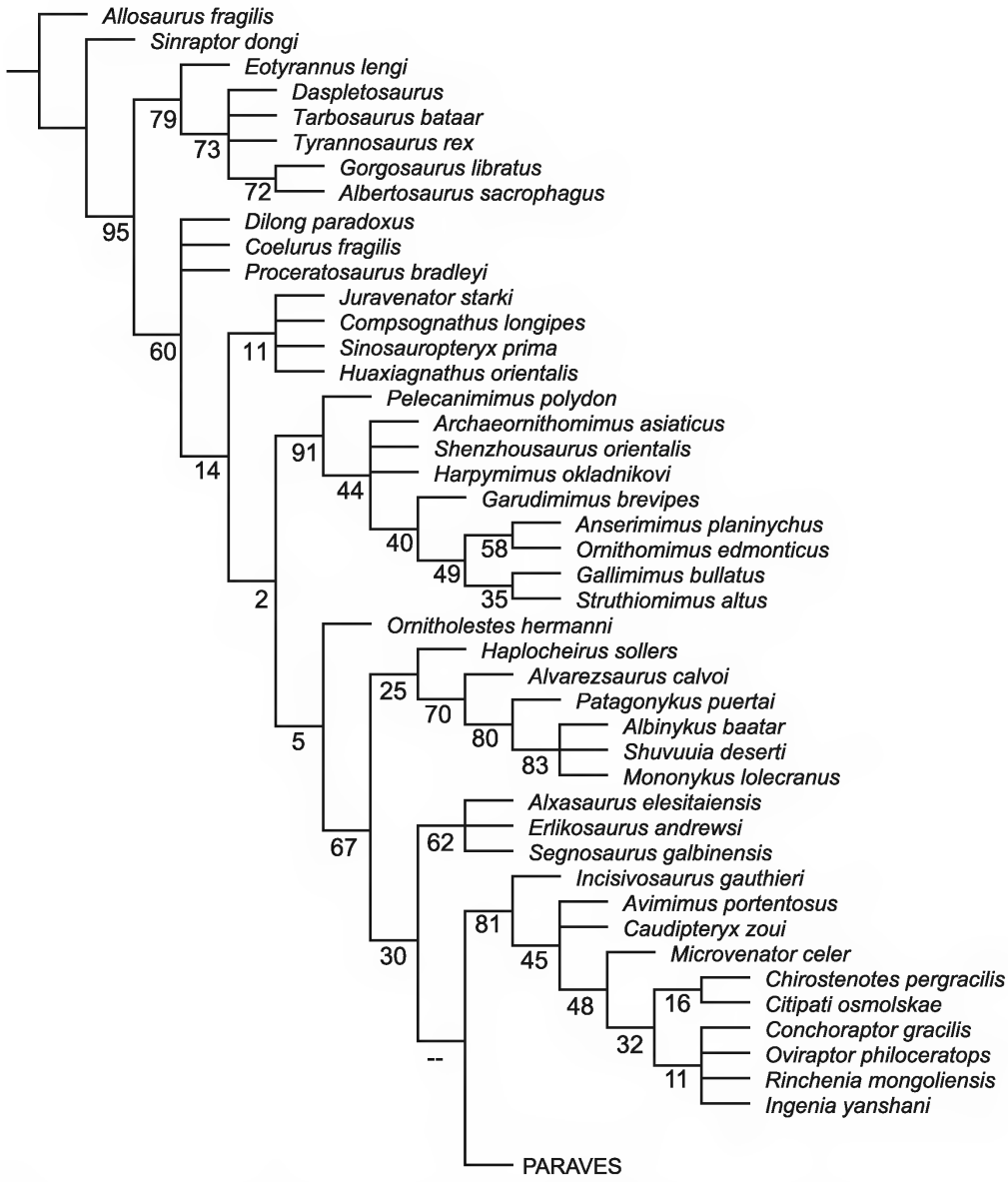


Fig. 66. Jackknife analysis. Strict consensus cladogram of basal coelurosaurs. Values indicate jackknife support reflected as GC frequencies derived from 1000 jackknife replicates with a character-removal probability of 0.20.

the most frequent contradictory group. Using raw frequencies is not recommended because there are cases in which groups lacking support have a frequency of 0.5 (Goloboff et al., 2003). GC frequencies are preferable because they reflect the balance between the amount of evidence that corroborates a given clade with the amount that falsifies that group.

The results from the entire dataset reflect a wide range of support for nodes across the entire tree (figs. 66–68). Unsurprisingly, coelurosaurian monophyly is extremely well supported (GC = 95) with little contradictory evidence. The basal Tyrannosauroidea clade is also well supported as is the less inclusive Tyrannosauridae node (GC = 79 and 73, respectively).

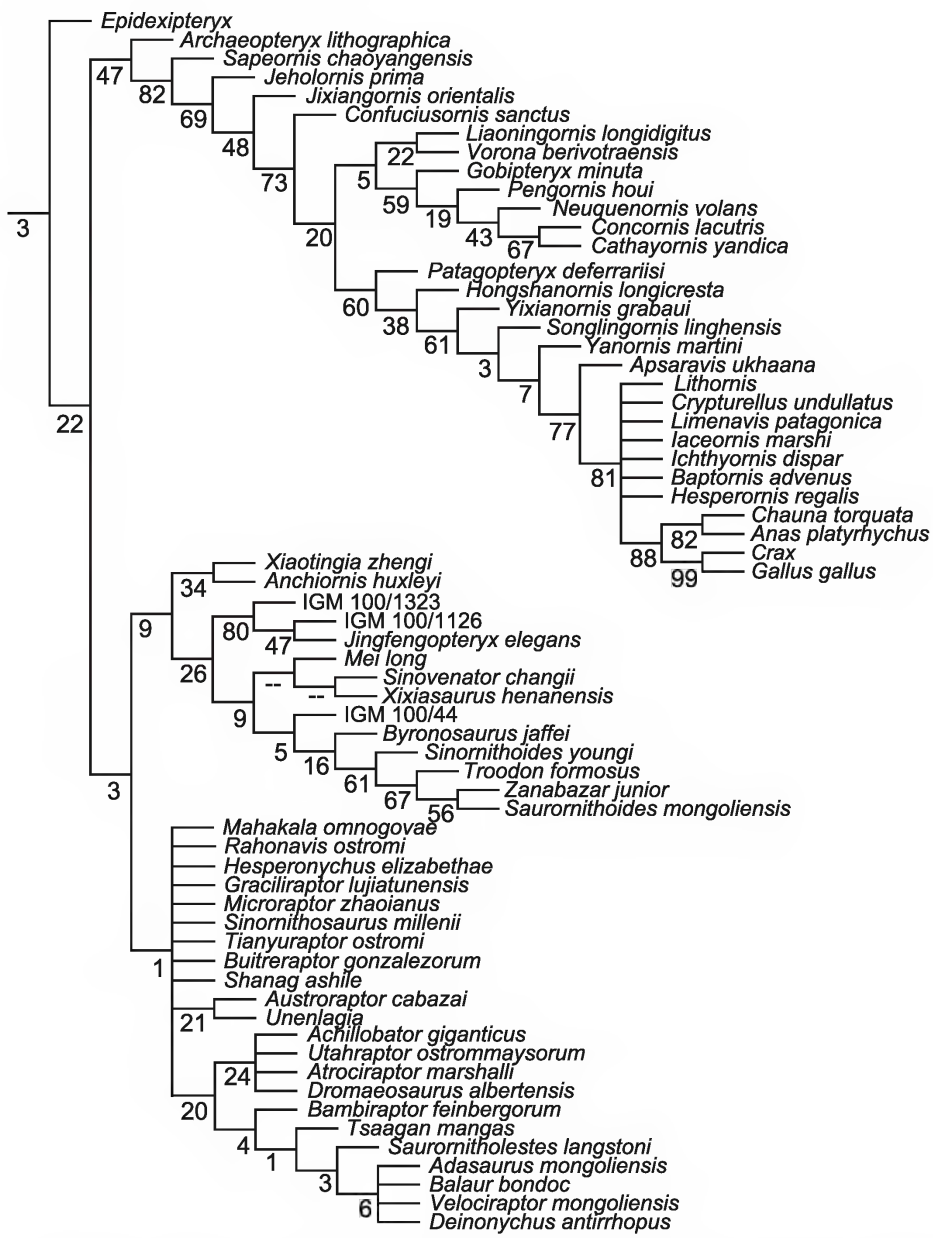


Fig. 67. Jackknife analysis. Strict consensus cladogram of paravians. Values indicate jackknife support reflected as GC frequencies derived from 1000 jackknife replicates with a character-removal probability of 0.20.

The node containing all coelurosaurs more derived than tyrannosauroids possesses little contradictory evidence (GC = 60). Most of the intervening nodes between *Proceratosaurus bradleyi*, Ornithomimosauria, and derived maniraptorans have extremely low support (GC values between 2 and 12). This is neither surprising nor very informative given that most of these nodes collapse in the strict consensus topology of the phylogenetic analysis due to the labile positions of *Proceratosaurus bradleyi*, *Dilong paradoxus*, and *Coelurus fragilis*. Compsognathidae monophyly has relatively high levels of

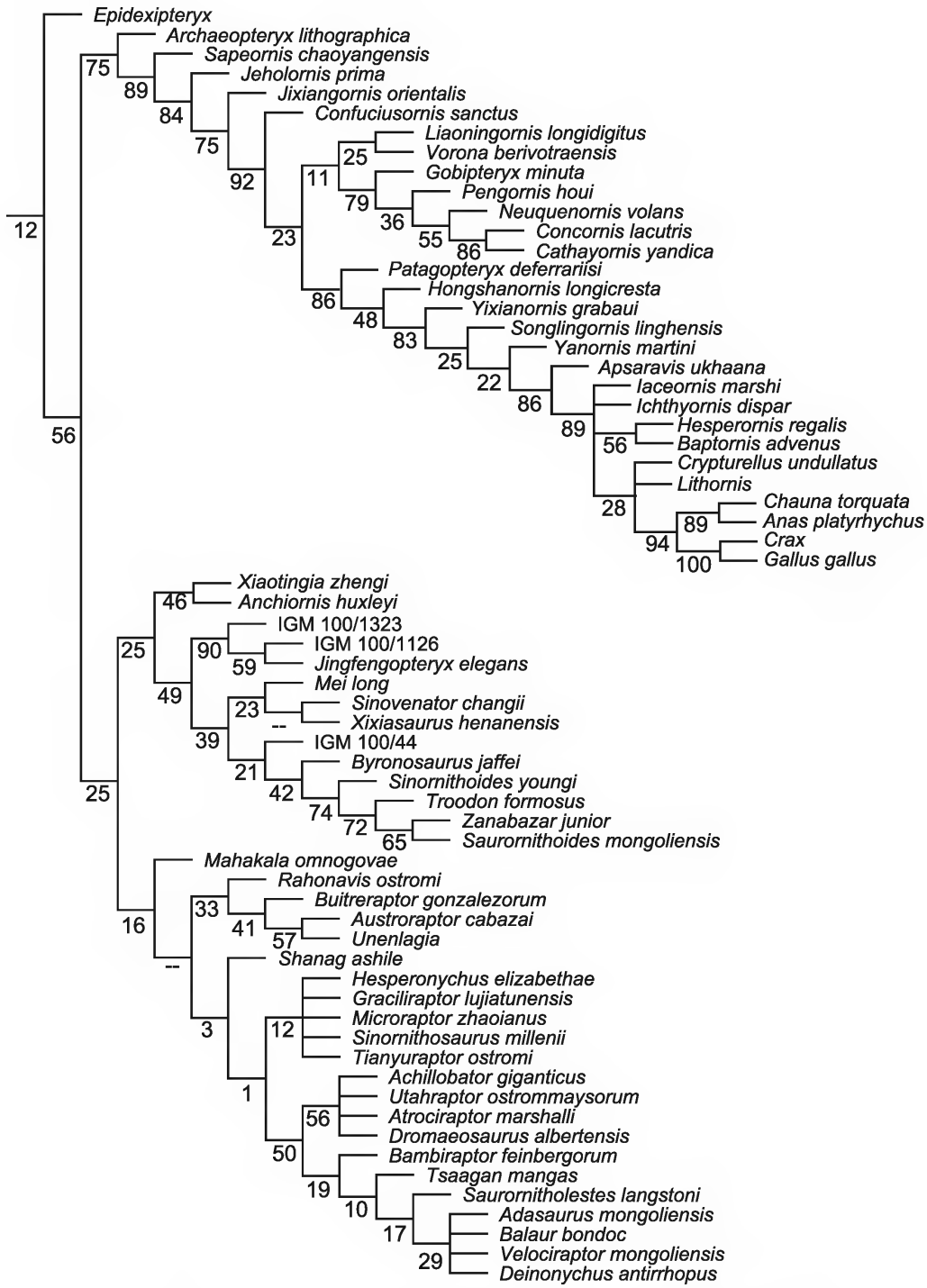


Fig. 68. Jackknife analysis. Reduced strict consensus cladogram of paravians. Values indicate jackknife support reflected as GC frequencies derived from 1000 jackknife replicates with a character-removal probability of 0.20.

contradictory character data (GC = 11), but Ornithomimosauria monophyly shows high jackknife support with little contradictory data (GC = 91). Most of the constituent ornithomimosaur clades are moderately supported (GC values in the 40s).

Maniraptora is poorly supported in the analysis (GC = 5). Most other derived maniraptoran clades, however, show surprisingly high levels of jackknife support. Alvarezsauroidea is moderate to weakly supported (GC = 25), but the less inclusive Alvarezsauridae and its constituent clades have high jackknife support (ranging from 70 to 83). The sister taxon relationship of *Patagonykus puertai* with *Shuvuuia deserti* and *Mononykus olecranus* is strongly supported (GC = 80).

The node containing the common ancestor of Alvarezsauroidea plus Paraves is well supported (GC = 67) whereas the next most derived node (i.e., Therizinosauria + Oviraptorosauria + Paraves) has only moderate-to-low jackknife support (GC = 30). Therizinosauria and Oviraptorosauria monophyly have high GC frequencies, 62 and 81 respectively. Less inclusive clades within Oviraptorosauria show moderate to low support. *Avimimus* + all more derived oviraptorosaurs has a GC value of 45, *Microvenator* + all more derived oviraptorsaurs has a GC value of 48, but clades more deeply nested than these nodes show higher levels of contradictory character data with GC values as low as 16 and 11.

The monophyly of Paraves is poorly supported (GC = 3) in part because of the placement of *Epidexipteryx* at the base of the clade. Analyses excluding *Epidexipteryx* find less contradictory data for the clade (GC = 54). The Avialae + Deinonychosauria node is also weakly supported with a GC value of 22. The Avialae node has moderate jackknife support (GC = 47). Deinonychosauria monophyly has significantly less support (GC = 3). The Troodontidae node has high levels of contradictory data (GC = 9), but most clades within Troodontidae have GC values between 50 and 80. Indeed, the new basal troodontid clade—Jinfengopteryginae—possesses some of the strongest jackknife support among troodontids, with a GC value of 80 and the *Xiaotingia* + *Anchiornis* clade has a GC value of 34.

Dromaeosauridae monophyly has weak jackknife support (GC = 1), and support for most clades within Dromaeosauridae is also quite weak. Only the Laurasian dromaeosaurid clade (GC = 20), Dromaeosaurinae (GC = 24), and the clade comprised of *Austroraptor* + *Unenlagia* (GC = 21) have jackknife frequencies at or above 20. Due to the conflicting position of several of the dromaeosaurid taxa in this analysis, the jackknife support was also explored analyzing the entire dataset, but summarizing the node stability while ignoring the position of the most unstable taxa (i.e., *Pyroraptor olympius* and *Limenavis patagonicus*) (fig. 68). This result therefore evaluates the node stability ignoring the poorly known and problematic taxa mentioned above. As the procedure matched the elaboration of the agreement subtree (fig. 58) above (i.e., considering the information of these taxa for the analysis, allowing their information to influence the interrelationships of all taxa, but excluding them from the consensus to see the underlying structure of the data), the support values obtained through this method are directly comparable with the tree in figure 58.

This reduced jackknife analysis shows higher GC values for Deinonychosauria (GC = 25) and both Troodontidae (GC = 25) and Dromaeosauridae nodes (GC = 16). The node containing all dromaeosaurids more derived than *Mahakala omnogovae* is very weakly supported and does not show up in the jackknife analysis. However, other dromaeosaurid nodes that were poorly supported in the total analysis show higher support values. The Laurasian dromaeosaurid clade (GC = 50), Unenlagiinae (GC = 33), and the clade composed of *Unenlagia* + *Austroraptor* (GC = 57) all show moderate GC values. Velociraptorinae continues to have low support (GC = 19), but Dromaeosaurinae monophyly continues to have generally low levels of contradictory data (GC = 56).

Within Avialae, basal nodes show extremely high support (GC values between 92 and 75) with little contradictory data present. In the total analysis, Pygostylia has moderate to high support (GC = 73), but in the reduced jackknife analysis this node also has almost no contradictory data (GC = 92). Ornithothoraces and Enantiornithes are weakly

supported in the total analysis (GC values of 20 and 5, respectively), but support in the reduced analysis is a bit higher (23 and 11). The subclade of enantiornithines including *Neuquenornis* + *Gobipteryx* + *Concornis* + *Cathayornis* + *Pengornis* is highly supported (GC = 79) and the *Liaoningornis* + *Vorona* clade has weak, but not terrible support (GC = 25). Euornithes is highly supported with little contradictory data (GC = 86) as are the first few more derived euornithine nodes. The *Apsaravis* + all more derived euornithines node has very little data contradicting this relationship (GC = 89). Unsurprisingly, the jackknife support of many of the most derived avialan nodes is weak for both the total and reduced jackknife analyses because of the various positions taken by *Limenavis* and *Iaceornis*, and failure to consistently depict *Lithornis* and *Crypturellus* as a monophyletic Paleognathae. Neognathae monophyly, however, is supported with a GC value of 94.

Bremer support was calculated using negative constraints as employed by the BREMER.RUN script supplied with TNT. As in the jackknife analysis, two consensus trees were estimated from the set of 100,000 suboptimal trees. The first was a strict consensus including all the analyzed taxa, as is typically done in this sort of analysis (Bremer, 1994). The second was also a strict consensus, but now ignoring the alternative position of the conflictive and incompletely known taxa discussed above. As in the case of the reduced jackknife support, the 100,000 suboptimal trees were found analyzing the entire dataset allowing their information to influence the results. As in the previous case, their exclusion from the strict consensus used to summarize the Bremer support reveals some structure to the data that otherwise remains hidden.

The Bremer support analysis including the entire set of coelurosaurian taxa results in a consensus tree with minimal support for most of the nodes of the tree. Most nodes have extremely low Bremer values, ranging between 1 and 2 (figs. 69–71). The exceptions to this are the Ornithomimosauria node (Bremer value = 4), the Oviraptorosauria node (Bremer value = 3), the *Patagopteryx* + derived euornithine node (Bremer value = 3), the *Yixianornis* + derived euornithine node (Bremer value = 4), and the three Neognathae nodes. All of these nodes with high Bremer support also showed very little contradictory data in the jackknife analysis discussed above. Within Deinonychosauria, no node has a Bremer value higher than one, which is not altogether surprising given the uncertainty in the position of *Pyroraptor olympius*.

The Bremer support values of the nodes described and diagnosed above are generally not much higher when the alternative positions of the uncertain taxa, excluded in the reduced strict consensus, are ignored (i.e., *Pyroraptor olympius* and *Limenavis patagonicus*). The exception to this is for nodes within Paraves, which again is not altogether unsurprising, because this is the clade within which these most labile taxa have uncertain positions. As in the case of the jackknife analysis and the Bremer analysis of the complete dataset, the avialan nodes of Paraves are most strongly supported (fig. 71) relative to other paravians, suggesting the robustness of the evidence favoring Avialae monophyly and successively more derived positions of *Sapeornis chaoyangensis*, *Jeholornis prima*, *Jixiangornis orientalis* to the *Confuciusornis* + all more derived avialan node (all with Bremer values of 2).

The reduced Bremer support analysis also indicates that the most poorly supported nodes in the Bremer analysis are generally the same as those in the reduced jackknife analysis. As in the reduced jackknife analysis, Bremer support for the basal nodes of Troodontidae and Dromaeosauridae show little improvement over the total analysis. Troodontidae shows a Bremer value of 1 as does Dromaeosauridae. The monophyly of the basal troodontids composing Jinfengopteryginae is supported in the reduced Bremer analysis with Bremer value of 2, which is in contrast to the high jackknife support (GC = 90). On the dromaeosaurid side, the dromaeosaurid node excluding *Mahakala omnogovae* has a Bremer value of 1, as does the Laurasian dromaeosaurid node. The reduced jackknife analysis indicated generally weak support for Dromaeosaurinae and Velociraptorinae and the same is true for the reduced Bremer analysis. This suggests that whereas relationships among deinonychosaurs generally and dromaeosaurids in particular have begun to stabilize, the character

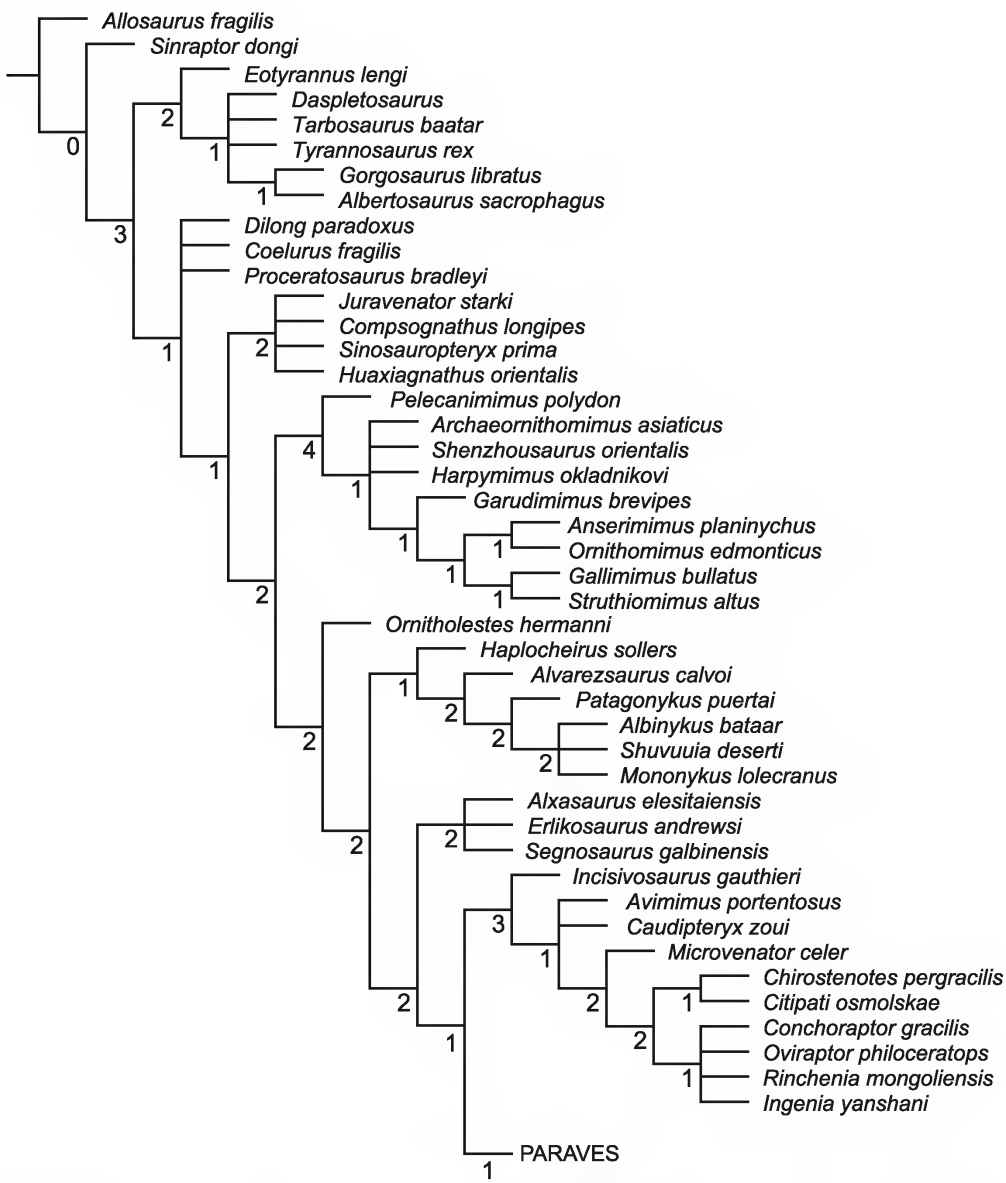


Fig. 69. Bremer analysis. Strict consensus cladogram of basal coelurosaurs. Values indicate Bremer support derived from the BREMER.RUN script supplied by TNT.

support for these nodes is weak and the addition of new data in the form of new fossils or new characters has the potential to overturn some of the clades discussed in the present study. The exception to this within Dromaeosauridae appears to be the unenlagiines, which have comparatively high Bremer support values. Unenlagiinae has a Bremer value of 2 the *Buitreraptor* + *Austroraptor* + *Unenlagia* node has a Bremer value of 3, and the *Austroraptor* + *Unenlagia* node has a Bremer value of 4.

DISCUSSION

Deinonychosaurian Monophyly: Strength and Sensitivity

Deinonychosaurian monophyly is well supported in the present cladistic analysis and has been consistently recovered in all

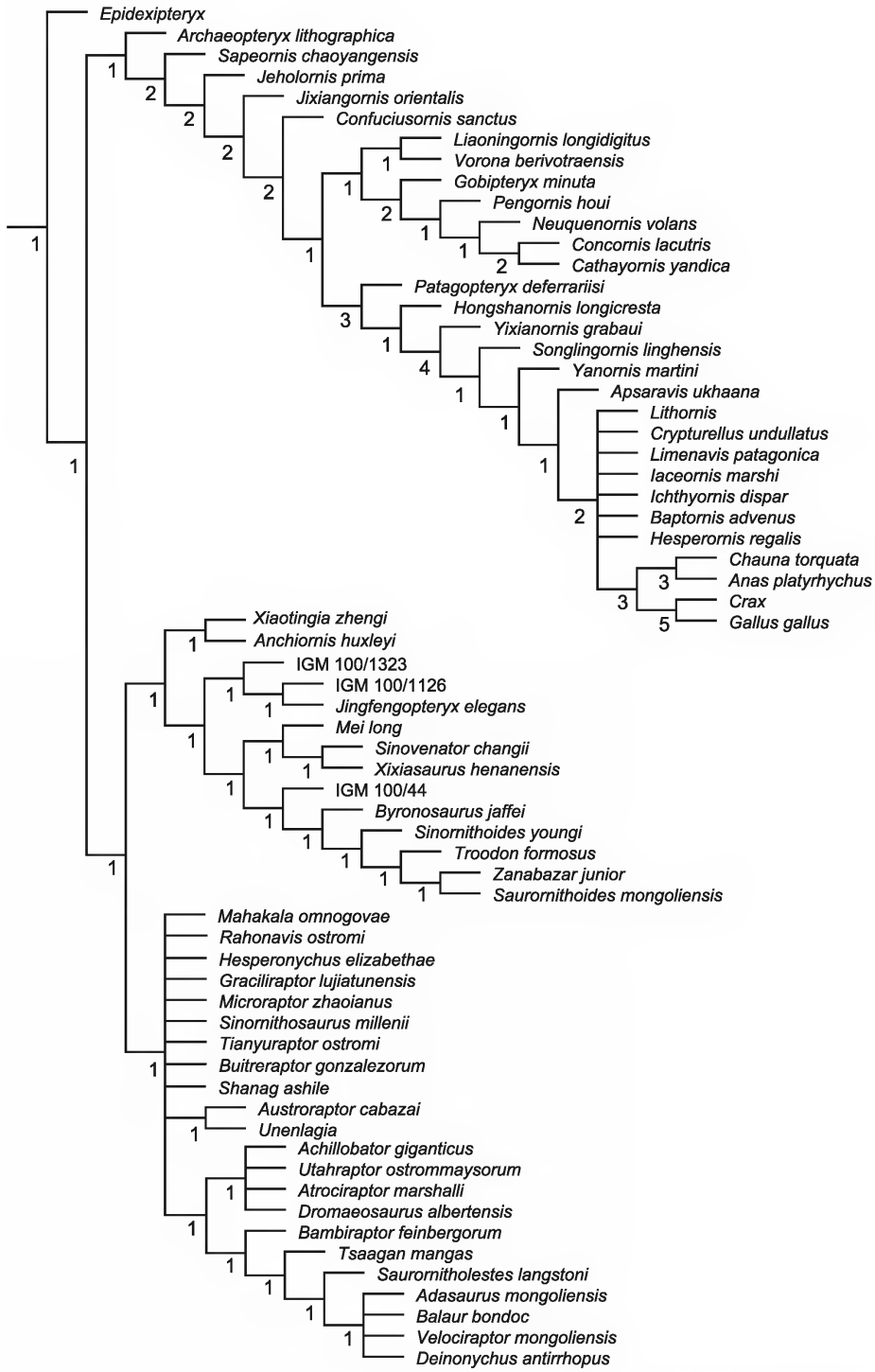


Fig. 70. Bremer analysis. Strict consensus cladogram of paravians. Values indicate Bremer support derived from the BREMER.RUN script supplied by TNT.

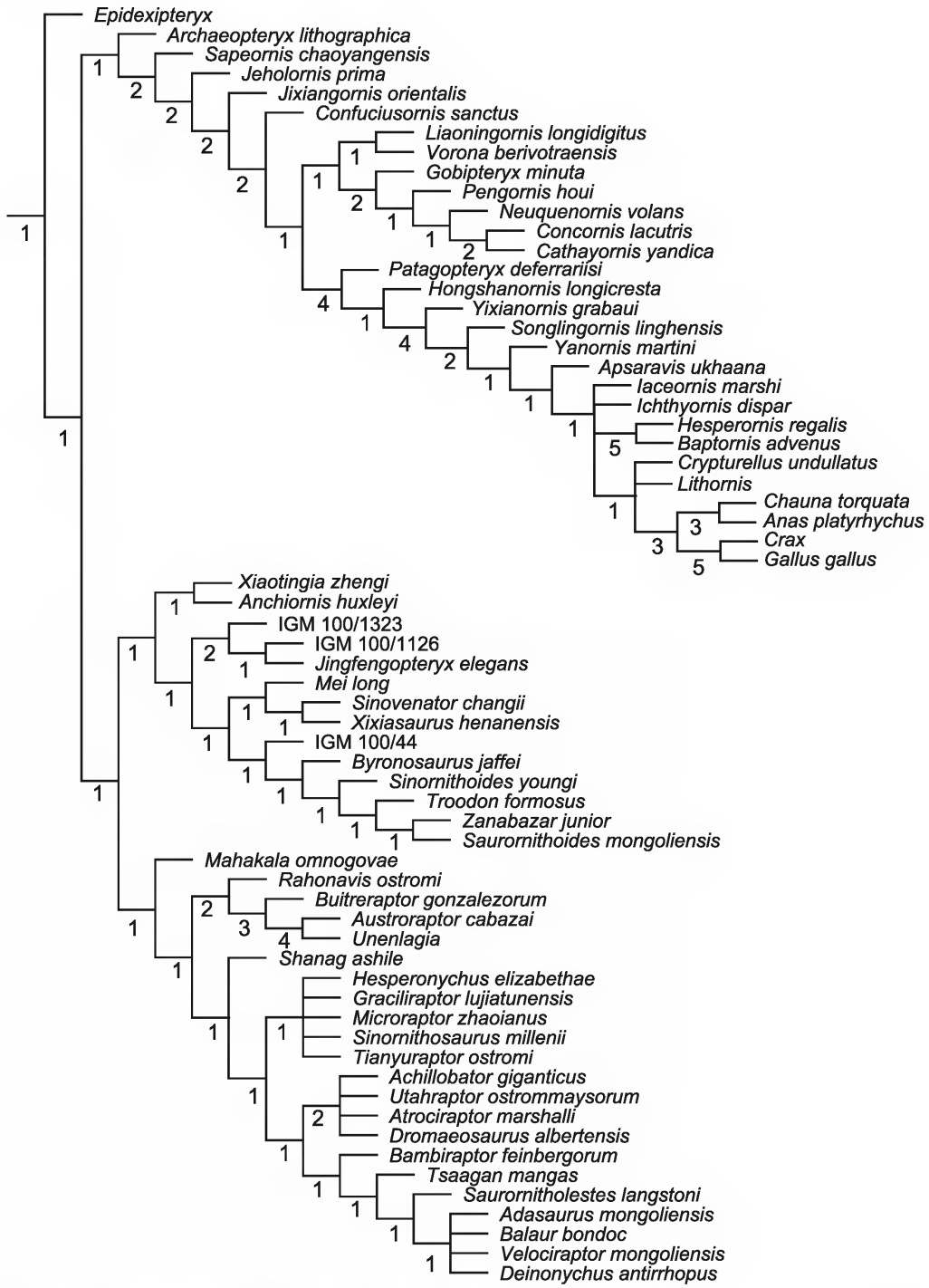


Fig. 71. Bremer analysis. Reduced strict consensus cladogram of paravians ignoring the alternate positions of *Pyroraptor*. Values indicate Bremer support derived from the BREMER.RUN script supplied by TNT.

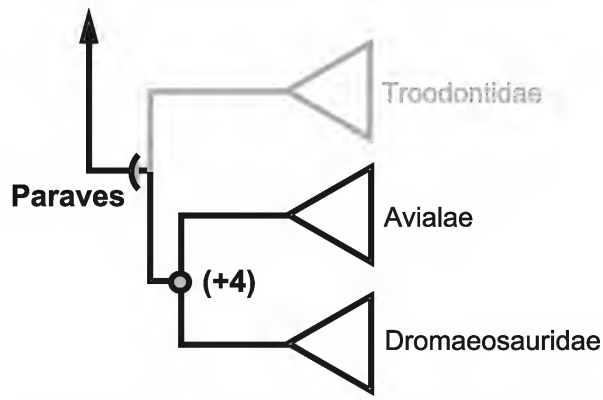


Fig. 72. Simplified cladogram showing manipulated paravian relationships. Constraining Dromaeosauridae to be sister group of Avialae requires 4 additional steps.

TWiG analyses after the original Norell et al. (2001) analysis. The few analyses, such as Senter (2004), that failed to find deinonychosaur monophyly tended to have poor taxonomic and character sampling relevant to the basal nodes of Troodontidae and Dromaeosauridae. When these deficiencies are accounted for (e.g., Holtz, 2001; Senter, 2007) deinonychosaur monophyly is recovered. Therefore, Deinonychosauria has proven to be one of the more consistently robust coelurosaur clades possessing clear, relatively nonhomoplastic synapomorphies.

The jackknife analysis conducted in the above chapter showed that there is only moderate level of evidence contradicting Deinonychosauria monophyly (GC = 25). However, the Bremer analysis showed that collapsing the Deinonychosaurian node requires accepting trees only 1 step longer than the most parsimonious trees. Exploring sensitivity to longer trees and the topologies they may entail illustrates possible topologies other than deinonychosaur monophyly (figs. 72, 73). Splitting Deinonychosauria, but retaining the division and monophyly of the three constituent paravian clades (Dromaeosauridae, Troodontidae, and Avialae) requires only 1 or 2 additional steps depending on the resulting topology. If Dromaeosauridae is constrained to be the sister taxon to Avialae, the resulting topology requires 4 additional steps beyond the most parsimonious reconstruction (fig. 72). On the other hand, only 1 additional step is required to place Troodontidae as the sister taxon to Avialae (fig. 73). These only slightly less parsimonious topologies could be interpreted as an indication of weakness in deinonychosaurian monophyly. We are inclined to interpret (and think it is more readily borne out by the data) that this is instead a reflection of the overall morphological similarity of the basal members of each paravian clade (e.g., compare *Mahakala* to IGM 100/1126 or *Archaeopteryx*).

Nonmonophyly of any of the three primary paravian groups is strongly unparsimonious. As an example, troodontid nonmonophyly is particularly illustrative. As context, troodontid similarities to basal avialans have been discussed in the past (Currie, 1987, 1995). Furthermore, Hwang et al. (2004a) raised the possibility of troodontid paraphyly relative to Avialae due to many potentially derived similarities among basal taxa (recovered by our analysis as members of the Jinfengopteryginae) and basal avialans. As illustrated in figure 74 troodontid paraphyly and particularly a Jinfengopteryginae + Avialae relationship is strongly unparsimonious requiring 12 steps more than the most parsimonious topology. This speaks to the robust nature of Troodontidae monophyly, even though there is low jackknife (GC = 25) and Bremer (Bremer value = 1) support.

Inclusion of Problematic Paravian Taxa

The Middle to Late Jurassic Chinese taxa *Epidendrosaurus ningchengensis*, *Epidexipteryx hui*, and *Pedopenna daohugouensis* have occupied various positions within Paraves

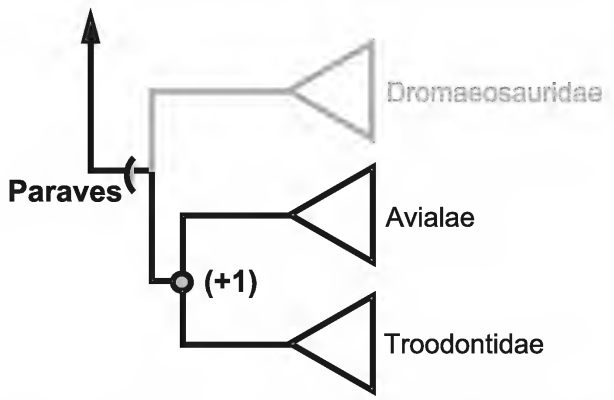


Fig. 73. Simplified cladogram showing manipulated paravian relationships. Constraining Troodontidae to be sister group of Avialae requires 1 additional step.

depending on the analysis. *Epidendrosaurus* has typically been recovered as a basal avialan either just outside the *Archaeopteryx* node (Senter, 2007; Zhang et al., 2008) or just inside the *Archaeopteryx* node (Choiniere et al., 2010), or in an unresolved position basally in Avialae (Xu and Zhang, 2005). *Epidexipteryx* has typically been recovered as the sister taxon to *Epidendrosaurus* forming a clade called Scansoriopterygidae (Zhang et al., 2008). The phylogenetic position of *Pedopenna* has been tested only by Xu and Zhang (2005) and was found in a polytomy with an unresolved avialan clade and deinonychosaurs.

Epidexipteryx: Inclusion of *Epidexipteryx* in our analysis resulted in a novel phylogenetic position for this taxon as a basal paravian outside of the split between deinonychosaurs and avialans, as was discussed above. *Epidexipteryx* resembles basal oviraptorosaurs in several respects, particularly in its cranial morphology. Zhang et al. (2008) noted some of these, drawing attention to the anteroposteriorly short but dorsoventrally tall skull, the posterodorsally displaced naris and anteroposteriorly long parietals. Likewise, the highly procumbent anterior dentition and the slightly downturned mandible compares favorably to basal oviraptorosaurs like *Incisivosaurus, Caudipteryx,* and putatively *Protarchaeopteryx*. Constraining *Epidexipteryx* as a basal oviraptorosaur requires only one additional step in our dataset (fig. 75). Three features support the inclusion of *Epidexipteryx* in Oviraptorosauria, which are caudal vertebrae without a transition point (char. 115.1), a dentary that has teeth only anteriorly (char. 220.1), and a first premaxillary tooth much larger than the succeeding teeth (char. 251.2). A tail without a transition point is unique to oviraptorosaurs and *Epidexipteryx* and premaxillary teeth greatly enlarged relative to other premaxillary teeth is unique to *Incisivosaurus*, *Protarchaeopteryx,* and *Epidexipteryx*.

Because all previous analyses found *Epidexipteryx* as a basal avialan, we tested this position using our dataset but constraining *Epidexipteryx* to this position. This constraint analysis was only two steps longer than the most parsimonious solution (fig. 75) indicating that there is some signal there. A single synapomorphy (less than 25 caudal vertebra: char. 121.2) supports this position. Therefore, moving the phylogenetic position of *Epidexipteryx* among paravian and the closely related oviraptorosaurs requires accepting only slightly less parsimonious topologies. The great similarity that exists among basal paravians, basal oviraptorosaurs, and *Epidexipteryx* leads us to caution that the precise phylogenetic position of *Epidexipteryx* requires additional work to understand the interesting, and highly derived, anatomy of this taxon as well as a better understanding of the character changes taking place near the split between oviraptorosaurs and paravians.

Epidendrosaurus: Exploratory analysis including *Epidendrosaurus* finds it a basal avialan (fig. 76A). A metatarsal I that articulates with the medial surface of the distal end of metatarsal II (char. 205.3) and a

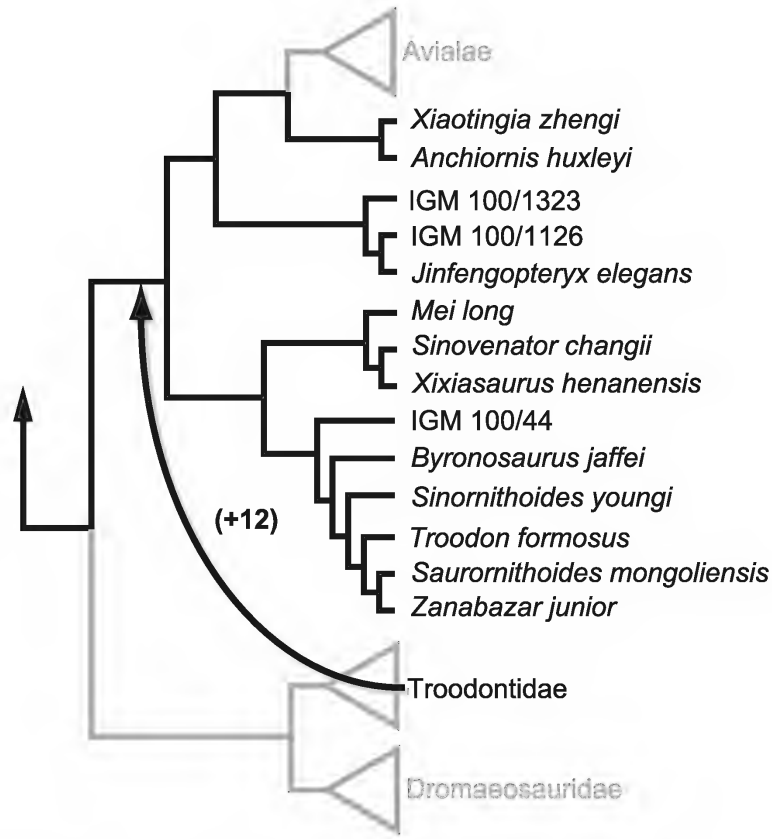


Fig. 74. Modified cladogram showing manipulated paravian relationships. Constraining Troodontidae to be paraphyletic relative to Avialae with *Xiaotingia* + *Anchiornis* and Jinfengopteryginae as successive sister taxa to Avialae requires 12 additional steps.

femur that is equal in length to or shorter than the ulna (char. 236.1) and the humerus (char. 266.2) support this relationship. As we have discussed earlier, we view it as problematic to include *Epidendrosaurus* in a phylogenetic analysis because of the extremely poor level of preservation, which results in much missing data, and the likely juvenile status of the holotype specimen. Our exploratory analysis reinforces this latter point. All three recovered synapomorphies are subject to ontogenetic changes and the observed morphology and proportions of the holotype of *Epidendrosaurus* may very well be different from its adult phenotype. We advise exclusion of *Epidendrosaurus* from primary phylogenetic analyses of paravians until more information is known about its adult morphology and a significant number of more cells in the data matrix can be populated.

It is important to note that inclusion of *Epidendrosaurus* in our analysis did not result in an *Epidendrosaurus* plus *Epidexipteryx* clade (i.e., Scansoriopterygidae). Constraining the monophyly of Scansoriopterygidae requires four additional steps and draws *Epidexipteryx* uptree, with the clade positioned basally among avialans (fig. 76B). A single feature, the absence of metatarsal V (char. 506.1), unites *Epidexipteryx* and *Epidendrosaurus* in our dataset.

Pedopenna: An exploratory analysis including *Pedopenna* results in over 100,000 most parsimonious trees of length 2031—certainly due to the fragmentary nature of the type, a unique specimen. The strict consensus of these topologies is largely unresolved above the alvarezsauroid node (fig. 77). Examination of the fundamental trees shows that *Pedopenna* is recovered in numerous

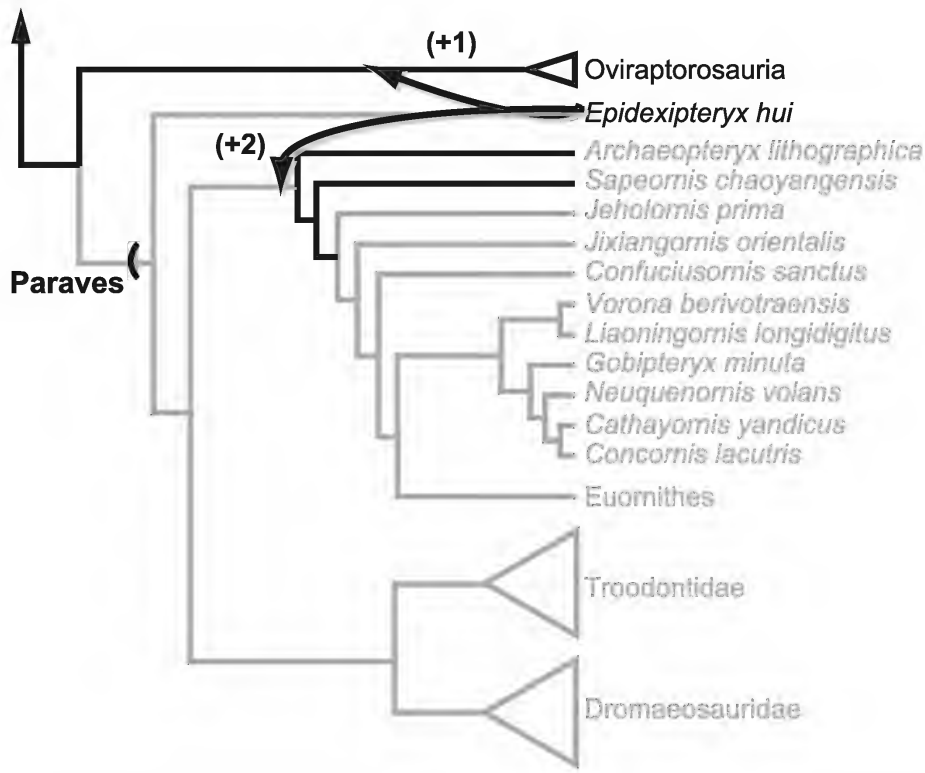


Fig. 75. Reduced strict consensus cladogram of Paraves + Oviraptorosauria showing the number of extra steps required to place *Epidexipteryx* as a basal avialan (2 steps longer), or to place it at the base of Oviraptorosauria (1 step longer). Analysis conducted in TNT using positive constraints.

places among oviraptorosaurs, therizinosaurs, and outside the paravian node near *Epidexipteryx* or sister to *Epidexipteryx*. Support for these various positions are typically weak (one synapomorphy) or nonexistentent (no unambiguous synapomorphies). The relatively global lability of *Pedopenna* among maniraptorans results in the reduced resolution of the strict consensus, but the underlying phylogenetic signal (consistent with the results from the primary analysis) remains as evinced from the Adam's consensus of these trees (fig. 78). At present it appears that too little is known about the morphology of *Pedopenna* to reliably place its phylogenetic position.

Is *Rahonavis* a Dromaeosaurid?

When *Rahonavis* was first described this small Malagasy paravian was thought to represent a transitional basal avialan (Forster et al., 1998; Chiappe, 2002). Subsequent species-level analyses (Norell et al., 2001; Hwang et al., 2002; Makovicky et al., 2003; Novas and Pol, 2005) continued to recover *Rahonavis* as the sister taxon to *Archaeopteryx lithographica* and *Confuciusornis sanctus*. However, as discussed in multiple places above, nearly all the traits proposed by Forster et al. (1998) and Chiappe (2002) are now known to have wide distributions within maniraptorans.

The discovery of *Buitreraptor gonzalezorum* by Makovicky et al. (2005) and the characterization of Unenlagiinae, the South American clade of dromaeosaurids, expanded the character data used for testing the phylogenetic position of *Rahonavis* and provided the foundation for, and was first to propose, *Rahonavis* as a dromaeosaurid and not an avialan. Successive iterations of the dataset used by Makovicky et al. (2005) continue to yield dromaeosaurid status for *Rahonavis*, even with the inclusion of

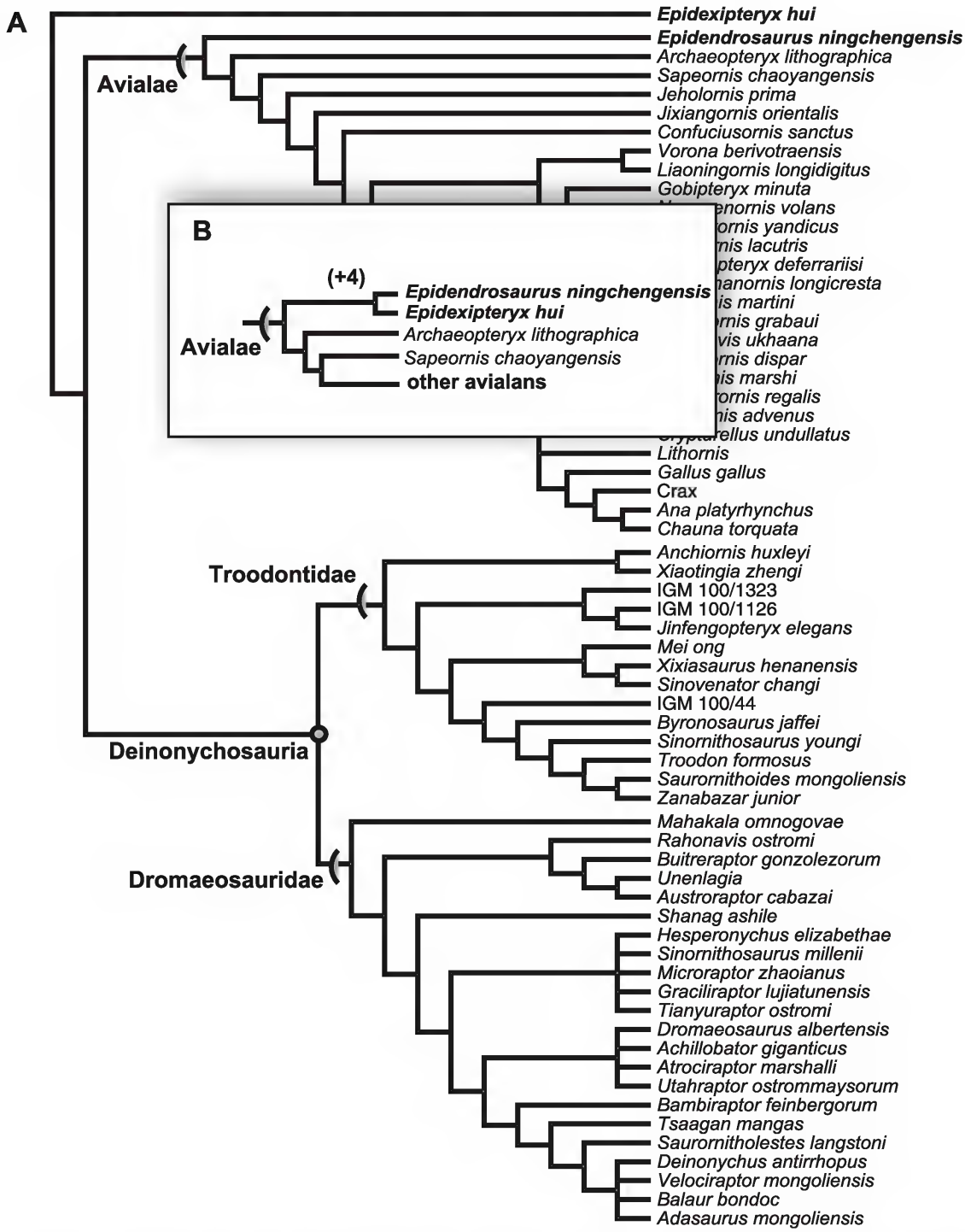


Fig. 76. Results from exploratory phylogenetic analysis including *Epidendrosaurus ningchengensis*. **A,** reduced strict consensus cladogram. **B,** detail of the base of Avialae showing the number of additional steps required to constrain *Epidendrosaurus* and *Epidexipteryx* are sister taxa.

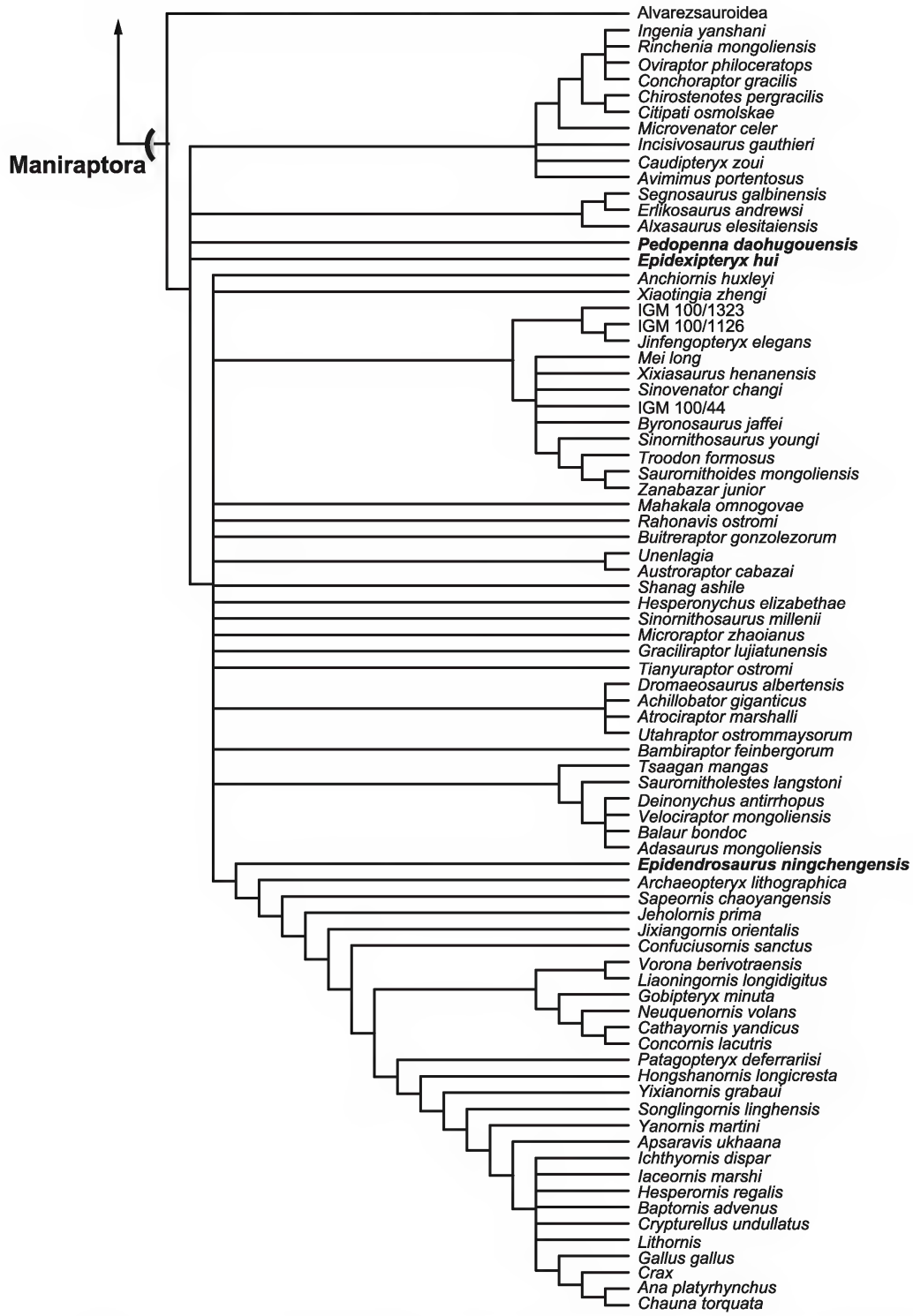


Fig. 77. Reduced strict consensus cladogram of exploratory phylogenetic analysis including *Pedopenna daohugouensis* and *Epidendrosaurus ningchengensis*.

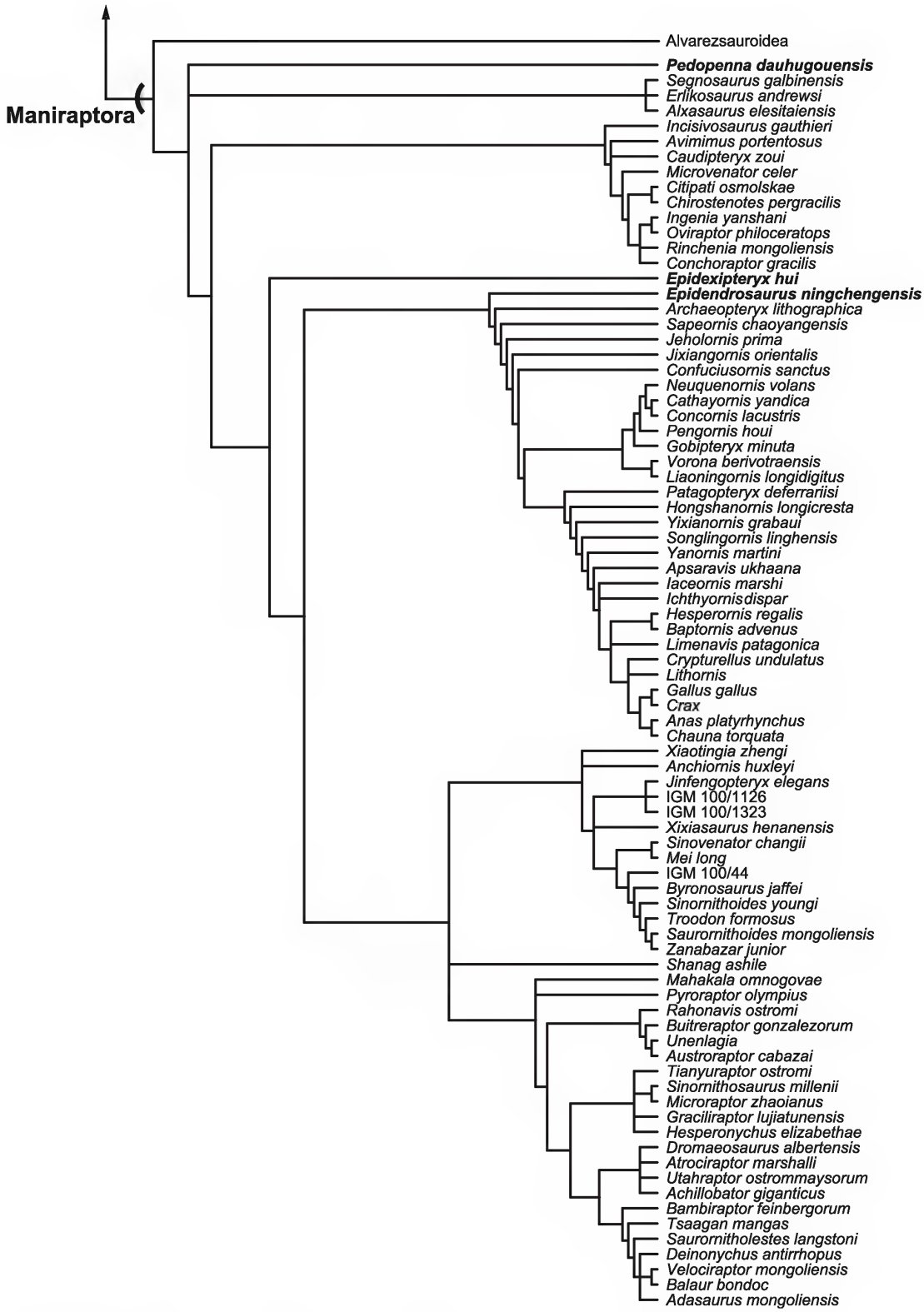


Fig. 78. Adam's consensus cladogram of exploratory phylogenetic analysis including *Pedopenna daohugouensis* and *Epidendrosaurus ningchengensis*.

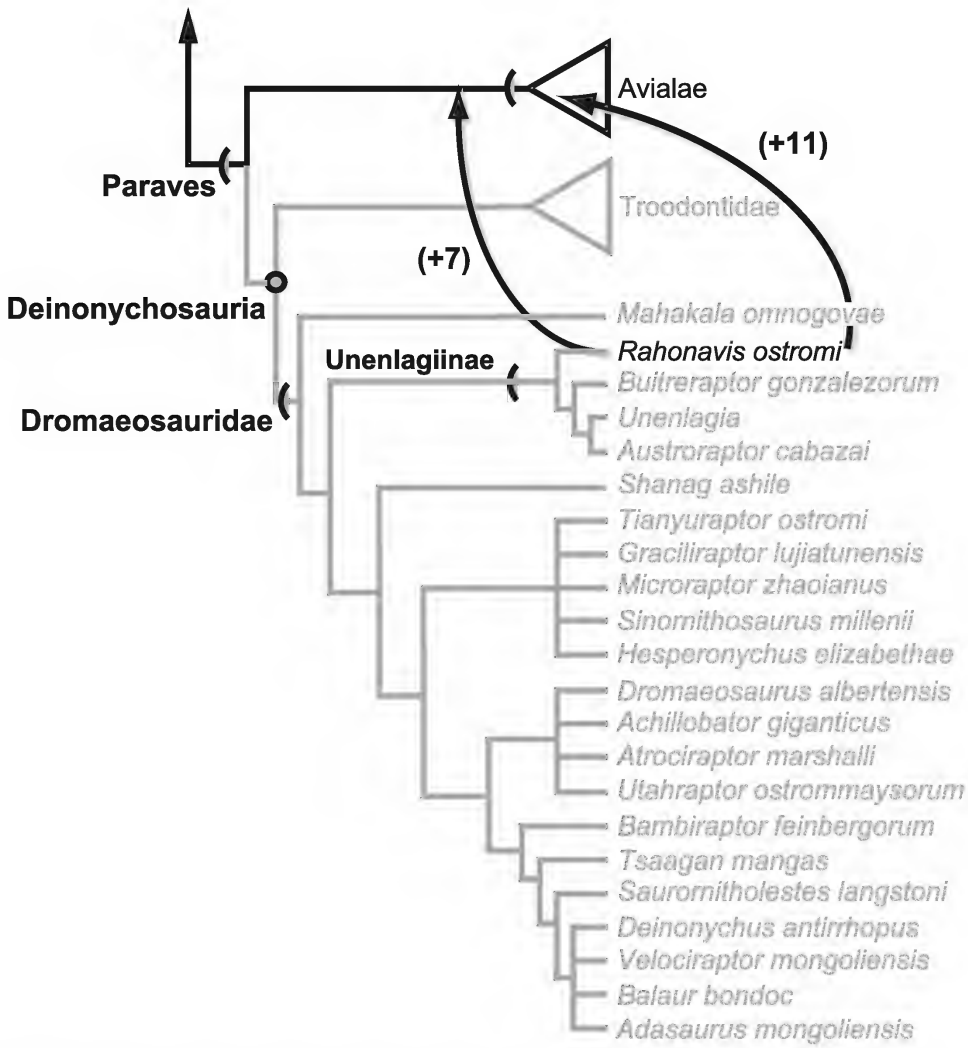


Fig. 79. Reduced strict consensus cladogram of Paraves showing the number of extra steps required to place *Rahonavis* as basal within Avialae (7 steps longer), or to place it within Avialae in a position more derived than *Archaeopteryx* (11 extra steps).

additional avialan taxa (Turner et al., 2007b). The remaining (and necessary) test for the affinities of *Rahonavis* rests on both the inclusion of basal avialans plus extensive character sampling of avialan synapomorphies and those that support the phylogenetic structure along the basal lineages of Avialae.

The dataset and the cladistic analysis conducted in our study provides this. Twenty-eight avialans and almost 200 morphological characters relating to avialan relationships were added. This substantial addition of data did not overturn the placement of *Rahonavis* with the Unenlagiinae clade of Dromaeosauridae. This relationship remains supported by at least six synapomorphies although support measures are somewhat weak. Constraining *Rahonavis ostromi* as a basal avialan requires seven additional steps beyond the most parsimonious topology, and constraining *Rahonavis* to a more derived placement within Avialae requires 11 additional steps (fig. 79). Taken together with the strong morphological support for the Unenlagiinae clade and strongly unparsimonious nature of an "avialan" *Rahonavis*, it

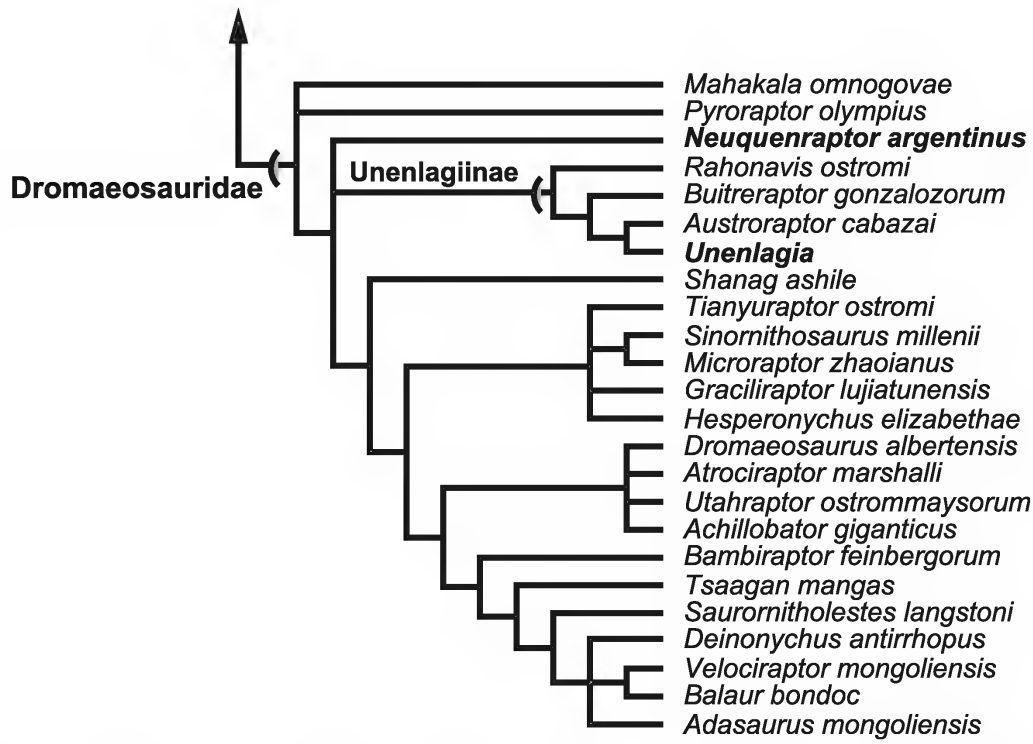


Fig. 80. Adam's consensus cladogram of Dromaeosauridae resulting from the exploratory analysis in which *Unenlagia* and *Neuquenraptor* are treated as separate terminal taxa.

has emerged that there is no reason to consider *Rahonavis* as a problematic taxon. Many of the features thought to be suggestive of avialan affinities are shared with its unenlagiine relatives and are most parsimoniously interpreted as convergent with derived avialans. Convergent evolution and mosaicism in character evolution among paravians is commonplace. So, to answer the question posed in this section—yes, *Rahonavis* is a dromaeosaurid.

Are *Neuquenraptor* and *Unenlagia* the Same Taxon?

Although discussed above in evaluating the validity of the various dromaeosaurid species, the question whether *Neuquenraptor* and *Unenlagia* are the same taxon proves difficult to answer, let alone to answer definitively. We continue to feel that this is an important issue in dromaeosaurid evolution, although we will argue that it is not as critical as it once was. Because we lack the necessary fossils for each taxon to directly compare the morphology of overlapping elements (currently limited to femora and pedal unguals of digit II), we instead pose the related question—does Unenlagiinae monophyly hinge on *Neuquenraptor* and *Unenlagia* being the same taxon? In Makovicky et al.'s (2005) original analysis and the following analyses of Norell et al. (2006) and Turner et al. (2007a, 2007b), such a taxonomic conclusion was necessary for the monophyly of the Gondwanan dromaeosaurids. By including new information from *Unenlagia paynemili*, the contaxonomic status of *Neuquenraptor* and *Unenlagia* is no longer necessary for unenlagiine monophyly (fig. 80).

Scoring *Unenlagia* and *Neuquenraptor* as separate terminals results in a set of most parsimonious trees of the same length as the primary analysis. *Neuquenraptor* can occupy multiple placements across the base of Dromaeosauridae therefore collapsing the base of the clade in the strict consensus solution. However, Adam's consensus dem-

onstrates that the monophyly and membership of Unenlagiinae is unchanged. Due to the paucity of material for *Neuquenraptor argentinus* we don't view this alternate analysis of dromaeosaurids as a strong indication of the phylogenetic position of *Neuquenraptor* or of the viability or validity of the contaxonomic status on these two taxa. Instead, this analysis should be viewed as exploratory and should only definitely illustrate that Unenlagiinae monophyly no longer rests on the assumed contaxonomic status of these two Gondwanan taxa.

The ultimate resolution of this question depends on either the discovery of a large amount of additional material referable to one or both of these taxa, or in coelurosaur systematists converging on a consensus.

Does *Archaeopteryx* have a Hyperextensible Second Digit?

Some authors have raised the possibility that *Archaeopteryx* possessed a hyperextensible second pedal digit homologous to the condition in deinonychosaurs (Gauthier, 1986; Sereno, 1997, 1999; Paul, 2002; Mayr et al., 2005, 2007). This claim is important to explore because of its relevance to character optimization at the base of Paraves. If *Archaeopteryx* indeed has a highly derived modified hyperextensible second digit this would indicate that it was a wider paravian synapomorphy and is not unique to Deinonychosauria as has traditionally been thought, and as recovered in the phylogenetic analysis discussed here.

The most recent incarnation of this argument was proposed by Mayr et al. (2005). These authors proposed that the foot of *Archaeopteryx* possesses "a hyperextensible second toe, as in Deinonychosauria..." (Mayr et al., 2005: 1485; also see Mayr et al., 2007). This claim was based on observation of the 10th described specimen of *Archaeopteryx* (WDC-CSG-100) as well as citations of Gauthier (1986), Elzanowski (2002), and Paul (2002). This observation, however, is problematic. Gauthier (1986a) does not say that the second digit of *Archaeopteryx* is hyperextensible, just that the distal articular surface of pedal phalanx II-1 was enlarged. Contrary to Mayr et al. (2005 and 2007), Elzanowski said that *Archaeopteryx* lacked an enlarged articular surface and stressed that the digit might in fact be *hyperflexive*.

It is our view that, at best, the distal articular surface is perhaps dorsoventrally enlarged (e.g., the WDC and Eichstätt specimens based on personal observations (A.H.T. and M.A.N.). However, unlike the condition present in deinonychosaurs, the distal articular surface of phalanx II-1 of *Archaeopteryx* does not extend proximally on the shaft (see Ostrom, 1969a) and lacks a deep midline trochlea. The depression that is present is rounded in *Archaeopteryx* and the sides are rounded, not convex as in *Deinonychus antirrhopus* (Ostrom, 1969a) and other dromaeosaurids like *Velociraptor mongoliensis* (IGM 100/985) and even the size-appropriate *Mahakala omnogovae* (IGM 100/1033) (Turner et al., 2011). Furthermore, the phalanx is not compressed along the long axis in *Archaeopteryx lithographica* as it is in deinonychosaurs. *Archaeopteryx lithographica* also lacks a number of other characters associated with the modified hyperextensible digit II in deinonychosaurs—even similarly sized animals like *Microraptor*. For example, digit II-2 lacks a proximal ventral heel and the distal end lacks the very large and very deeply grooved ginglymoid articular facet. The dorsal displacement and deepening of the ligament fossae on the lateral and medial surfaces of the phalanx present in deinonychosaurs are also lacking in *Archaeopteryx lithographica*.

It is apparent that it is an overstatement to say that the foot of *Archaeopteryx* possesses a hyperextensible second toe as in deinonychosaurs. Nonetheless, Mayr et al. (2005) added a new character state to character 170 from the TWiG dataset. This character state (177.2) is "penultimate phalanx of digit II modified for hyperextension but ungual not hypertrophied." This additional character state was scored as present only in *Archaeopteryx*. Reformulation of this character is extremely problematic. First, it is phylogenetically uninformative because Mayr et al.'s state 2 is autapomorphic for *Archaeopteryx*. To provide phylogenetic structure, this character would have to be rearranged and ordered so as to treat this new character state as intermediate between a lack of

hyperextension to fully hyperextensible with an enlarged ungual. However, this is not necessary because *Archaeopteryx* does not have any morphology indicative of hyperextension in the penultimate phalanx of digit II (i.e., phalanx II-2). Mayr et al.'s (2005) discussion was about a possible enlarged distal trochlear surface on phalanx II-1. This character state is entirely unnecessary, because no such character state exists within the sampled taxa.

An additional point worth noting is that the dataset coopted by Mayr et al. (2005) was not constructed nor intended to elucidate the interrelationships within Avialae (only two definitive avialans were included) and the character sampling was not intended to address the questions about which Mayr et al. (2005) were drawing conclusions. In fact, two more recent versions of TWiG datasets had been published by the time of the publication of Mayr et al. (2005). Furthermore, even if we could corroborate the observations of Mayr et al. (2005), or Mayr et al. (2007) for that matter, they would not necessarily alter paravian topology. Adding a new character for the presence of an enlarged distal end of phalanx II-1 to the Makovicky et al. (2005) matrix just renders it a paravian synapomorphy subsequently lost in all avialans more derived than *Archaeopteryx* (with some reversals within the crown clade and even in stem taxa like *Patagopteryx*).

Xiaotingia and the Position of *Archaeopteryx*

Recently Xu et al. (2011) reported the discovery of an interesting new paravian dinosaur from Late Jurassic of China, which according to their phylogenetic analysis significantly alters our understanding of avialan origins. Most significantly the authors claim to demonstrate for the first time that *Archaeopteryx* (and its sister taxon *Wellnhoferia*) is not a member of the clade Avialae and therefore not a basal bird. Through their discovery of a new clade of paravians comprised of *Archaeopteryx*, *Xiaotingia*, and *Anchiornis,* more closely related to the deinonychosaurs, these authors challenge the orthodox view of *Archaeopteryx* as the basalmost bird taxon. Using the data published by Xu et al. (2010) we reanalyzed the new dinosaur *Xiaotingia* within our larger phylogenetic dataset that samples paravian diversity more comprehensively and instead find *Xiaotingia* a basal troodontid, sister to the very similar *Anchiornis*, and *Archaeopteryx lithographica* still residing at the base of Avialae (fig. 58).

Review of the Xu et al. (2011) matrix reveals some character scorings that we dispute. Xu et al. (2011) atomize the presence of an enlarged and hyperextensible second pedal digit into several traits (chars. 201, 320–322). Character 322 describes the development of the flexor attachment heel on phalanx II-2 in deinonychosaurian taxa with the incipient condition of having a laterally displaced, small heel as state 2, while the possession of the more derived, enlarged heel is designated as state 1. Although Xu et al. (2011) describe and figure a ventrolateral flange or heel on pedal phalanx II-2 of *Xiaotingia*, they score it as absent in their matrix. Likewise, they code only the incipient condition as present in two unenlagiine taxa, whereas they consider a number of basal troodontids, such as *Mei* and *Sinovenator,* and basal dromaeosaurids, such as *Microvenator,* as having the more derived, enlarged heel below the proximal articulation. Based on our own study of the relevant specimens, we disagree with these scorings and instead code *Xiaotingia*, *Mei*, *Sinovenator*, *Microraptor*, *Unenlagia*, and *Sinovenator* as having state 2. Even without treating this character as an ordered transformation series, we recover a slightly different topology with *Xiaotingia* and *Anchiornis* as basal troodontids. Although we still discover *Archaeopteryx* as closer to deinonychosaurs than to Avialae, this result draws into doubt Xu et al.'s (2011) contention that their result was predicated entirely on the inclusion of *Xiaotingia.*

Another trait, whose scoring we find contentious, is their character 366 that describes the relative position of the postorbital process of the jugal along the length of that bone. Xu et al. (2011) score the process as close to the middle of the bone (state 0) in *Epidexipteryx*, which we agree with, but they go on to consider the basal avialans *Jeholornis*, *Sapeornis*, and *Confuciusornis* as well as the unenlagiine *Buitreraptor* as sharing this

condition. Our study of these specimens, as well as their own figure 4, shows that the position of the postorbital process of the jugal is far closer to the caudal end of the bone in these paravian taxa, as it is in *Archaeopteryx*, *Xiaotingia*, and basal troodontids and dromaeosaurids. A reanalysis of the matrix combining changes in the scoring of this trait along with those in character 322 culminates in a strict consensus tree in which the position of Troodontidae, Avialae (without *Archaeopteryx*), Dromaeosauridae, and the Archaeopterygidae clade found by Xu et al. (2011) are fluid. The paravian node shows eight resolutions in the set of 231 MPTs (TL = 1511), only one of which places *Archaeopteryx* as closer to a clade other than Avialae. A majority rule consensus reveals that 89% of resolutions favor the traditional alignment of *Archaeopteryx* as the most basal avialan, with *Epidexipteryx* and *Epidendrosaurus* grouping with oviraptorosaurs with an equal frequency (fig. 81). A possible relationship between these two enigmatic Middle Jurassic taxa and oviraptorosaurs has been previously proposed by Xu et al. (2009), although it was not tested at the time. As discussed above, an oviraptorosaur status for these two taxa is only one step longer than the most parsimonious trees from our matrix.

Lee and Worthy (2011) recently reanalyzed the Xu et al. (2011) dataset using maximum likelihood and Bayesian optimality criteria. They recovered *Archaeopteryx* at the base of Avialae, and attributed the support for this position as coming from fewer, but less homoplastic characters than those recovered under maximum parsimony as supporting a position closer to Deinonychosauria. Other parts of their recovered topology conflict significantly with the parsimony results, however, a point Lee and Worthy (2011) did not comment on. Major discrepancies include paraphyly of Tyrannosauroidea and a more derived, but stratigraphically less congruent, position for *Epidexipteryx* and *Epidendrosaurus* among Avialae. This leaves some question as to whether the differences are due to opposing resolutions of conflicting characters resulting from different optimality criteria or uneven evolutionary rates, which in this case translate to uneven character sampling across the tree. We explored this question by analyzing the data with parsimony using implied weighting (Goloboff, 1993), which downweights characters with increasing homoplasy. The results (9 best-fit trees for weight k = 3; fit score 164.72) placed *Archaeopteryx* within Avialae as more derived than *Epidexipteryx* and *Epidendrosaurus*, with *Xiaotingia* and *Anchiornis* posited as basal troodontids. Overall, the results conflict less with those from the unweighted parsimony analysis than those found by model-based analysis, although a couple of taxa with copious missing data (*Hagryphus*, *Haplocheirus*) exhibited anomalous affinities.

Taken altogether, these results show that it may be premature to declare *Archaeopteryx* a nonavian theropod. Much hinges on the exact position of the Middle Jurassic taxa *Epidendrosaurus* and, in particular, *Epidexipteryx*. These taxa share with oviraptorosaurs and basal avians a foreshortened rostrum, highly modified mandible, and reduced, unserrated dentition. A number of the relevant traits of the dentition and mandible have recently been identified as representing a homoplastic suite of characters that correlate with herbivorous habits (Zanno and Makovicky, 2011) and evolve independently in multiple maniraptoran lineages including oviraptorosaurs and avialans. Thus, it is possible that the phylogenetic result offered by Xu et al. (2011) is driven in part by adaptive ecological traits, a fact supported by the implied weights analysis and, to a less certain degree, by the model based analyses of Lee and Worthy (2011).

It is nevertheless also clear that the mosaic of character transformations surrounding avialan origins and evolution is far more complex than was appreciated just a few years ago. Taxa such as *Xiaotingia*, *Epidexipteryx*, and others play a significant role in elucidating these patterns, whether they lie directly on the avialan lineage or occupy position immediately adjacent to it.

Assembly of the Avian Shoulder Girdle

Our phylogenetic hypothesis for basal avialans within the broad context of other paravians, and the basal placement of *Sapeornis* among long-tailed avialans in particular, gives insight into the sequence of

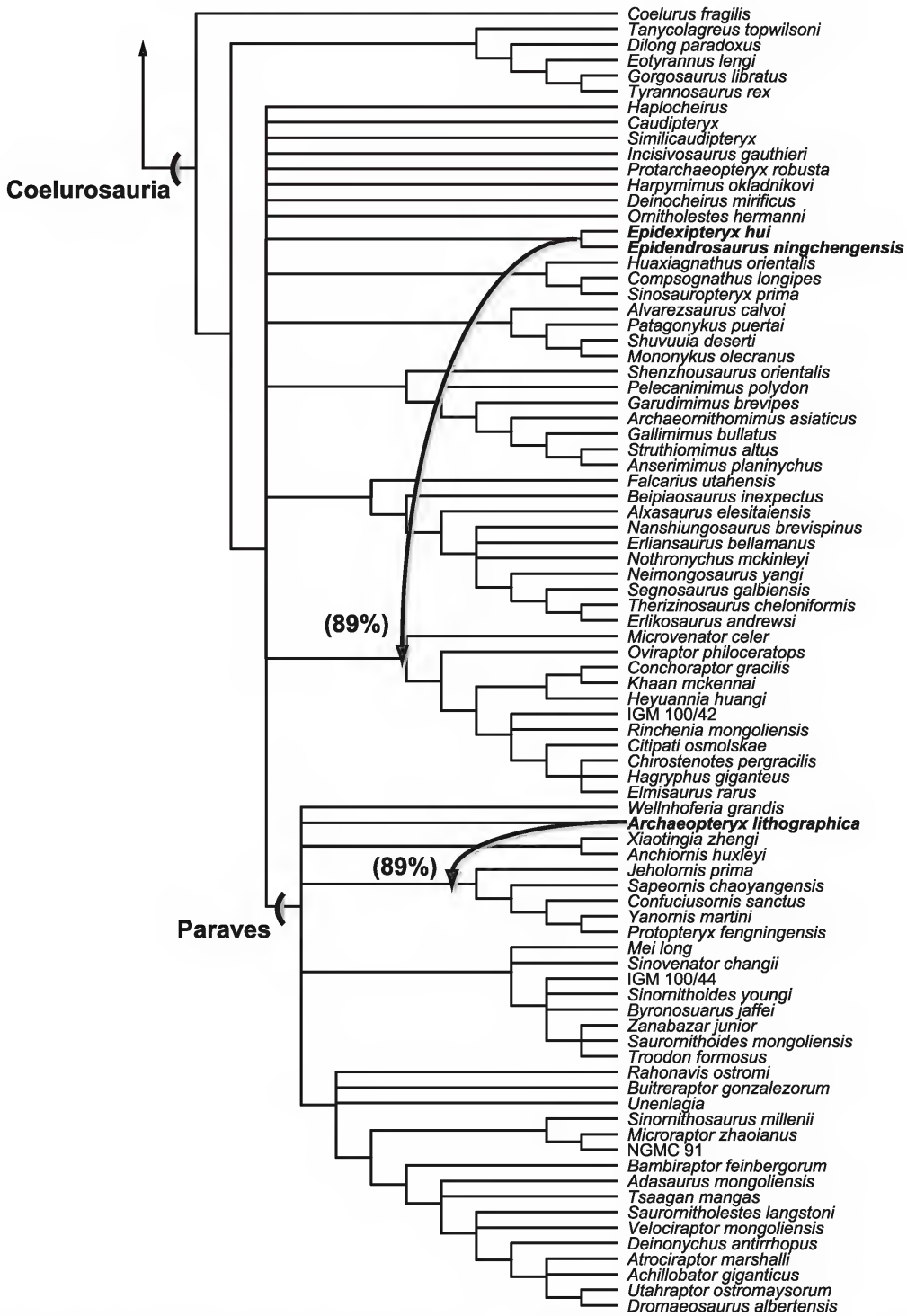


Fig. 81. Strict consensus cladogram of Coelurosauria based on the Xu et al. (2011) matrix having modified the scorings for their characters 322 and 366. Percentages indicate the frequencies of occurrence in the set of most parsimonious trees for the positions indicted by the arrows.

morphological changes that took place to restructure the avialan shoulder girdle. Like so many other features of the "bird" body plan (feathers, reproductive biology, etc.) the pattern that emerges is one of a sequential acquisition of modern "avian" features (fig. 81).

Plesiomorphically for paravians the coracoid is subquadrangular in shape (char. 136.2) and it articulated with the scapula along a simple flat sutural surface (char. 339.2). The glenoid facet in most paravians is located dorsal to or at the same level as the acrocoracoid process (= biceps tubercle) (char. 347.0) and the angle between scapula and coracoid is more than 90° (char. 351.0). Additionally, most paravians possess ossified sterna (char. 457.1), but the two plates usually do not coossify (char. 128.0). Most dromaeosaurids and troodontids exhibit this shoulder girdle architecture. Moreover, the basal avialans *Archaeopteryx lithographica* and *Sapeornis chaoyangensis* exhibit this same paravian-grade suite of morphological features with the exception that apparently in these two taxa the sternum never ossifies (the structure originally identified as a sternum in the Munich *Archaeopteryx* specimen is in fact a coracoid [Wellnhofer and Tischlinger, 2004]). Therefore, in overall construction the basal avialan shoulder girdle shows no morphological changes associated with increased stabilization.

Although derived in many aspects of the humerus, hand, and tail, *Sapeornis* shows little deviation from the plesiomorphic paravian condition in its shoulder girdle construction. It is not until the *Jeholornis* node that the shoulder girdle begins to take on more of a modern aspect. It is at this point in avialan evolution that the coracoids nascently become strutlike in morphology (char. 136.3). A number of other changes appear in concert with the elongation of the coracoid. The scapula and coracoid articulation takes on a "ball and socket" conformation with a pit-shaped scapular cotylus developed on the coracoid and coracoidal tubercle developed on the scapula (char. 339.0). The glenoid facet of the coracoid migrates ventral to the acrocoracoid process (char. 347.1) and the angle between coracoid and scapula at the glenoid is 90° or less (char. 351.1). It is also in *Jeholornis prima* that we first see ossified sternal plates (as in most other paravians) (char. 457.1), although they remain unfused to each other (char. 128.0).

Several of these features are correlated with increased rigidity of the shoulder girdle. The proximodistal elongation of the coracoid marks the beginning of the element's role as a compressive strut between the wing and the sternum like is seen in modern birds (Gray, 1968; Pennycuick, 1967). Similarly, the ossification of the sternal plates is an important corollary in the increased bracing system of the shoulder girdle (given that the forces directed through the coracoid are transmitted to the sternum). Also ossified sternae distribute compressive forces to the rib cage through the sternal ribs, so all the forces are not contained in the anterior part of the thoracic cavitly. The dorsal placement of the acrocoracoid process and the reduced angle between the scapula and coracoid served to redirect the acrocoracohumeral ligament and thereby provide incipient passive shoulder stabilization (Baier et al., 2007).

We do not see fusion of the ossified sternal plate on the midline (except in apomorphic taxa like some oviraptorosaurs and alvarezsaurs) (char. 128.1) until *Jixiangornis*. Fusion of the sternal plates into a single sternal element further strengthens the role the sternum played in bracing the shoulder girdle and absorbing the forces redirected to it through the coracoid (by restricting ventral midline flexion).

The pattern of trait evolution at the base of Avialae highlights the sequential nature of the acquisition of "avian" shoulder girdle features among basal birds. This pattern indicates that many of the features involved in shoulder stabilization and compressive force redirection had not yet evolved in the earliest avialans like *Archaeopteryx* and *Sapeornis*. Others characters involved in this system, like the furcula, have ancient origins within theropods (Nesbitt, et al., 2009). It wasn't until *Jeholornis* and *Jixiangornis* that a bracing system like that seen in modern flyers evolved in an incipient form. This is again more evidence that the powered flight that we see in modern avians is not comparable with the "volant" activity that perhaps existed in basal avialans.

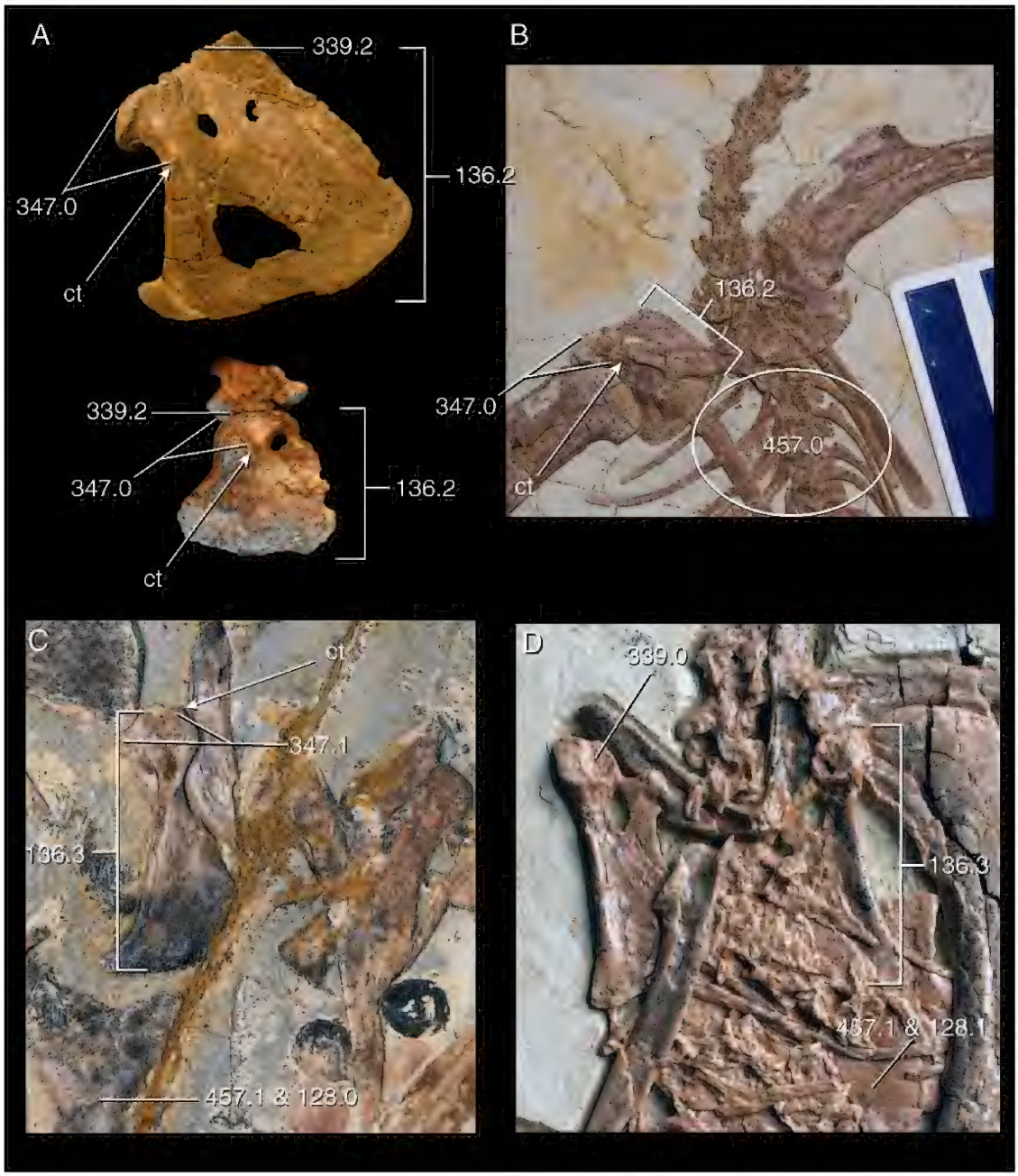


Fig. 82. Character changes associated with avialan shoulder girdle evolution. **A,** right coracoid of *Deinonychus antirrhopus* (YPM 5236; top) and *Sinovenator changii* (IVPP 12583; bottom); **B,** *Sapeornis chaoyangensis* (IVPP V13396) in ventral view; **C,** *Jeholornis prima* (IVPP V13274) in ventral view; **D,** *Jixiangornis orientalis* (CAGS uncataloged) in dorsal view.

CONCLUSIONS

The morphological gap between the paravian clades has blurred to the point that basal dromaeosaurids, troodontids, and avialans are nearly indistinguishable from one another, and in life these animals would appear extremely similar. However, important

morphological divisions exist that allow us to understand the basic relationship between these three clades. This study was undertaken with the intention of reviewing and revising dromaeosaurid systematics and taxonomy, supplying an extensive morphological data matrix for paravian theropods, and discussing the phylogenetic relationships derived from that data matrix. Taxon sampling within Paraves is the most exhaustive to date, but the phylogenetic hypotheses discussed herein will certainly not be the last word on paravian or coelurosaurian relationships. Indeed, changes and additions to similar data matrices are already yielding interesting results within the various clades of Coelurosauria. Moreover, the potential for new discovery that will modify these results is a given.

Paraves is an extraordinary clade with an extant diversity of nearly 10,000 species. The early radiation of this clade is first picked up in the fossil record in the Middle Jurassic and Early Cretaceous, and witnessed a plethora of taxa of remarkably similar body types within the basal members of the constituent clades Avialae, Dromaeosauridae, and Troodontidae. Because of their importance for understanding the evolution of avian flight and the rapid but divergent body size trajectories exhibited by the paravian clades, dromaeosaurids, troodontids, and avialans remain some of the more important clades for paleontological study. Extinct paravians highlight the important role fossils play in understanding the complex biology of modern organisms.

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APPENDIX 1

Specimen List

Collection numbers of the specimens that were revised firsthand by the authors are added after the bibliographic reference.

Achillobator giganticus (Perle et al., 1999; FR. MNUFR-15)
Adasaurus mongoliensis (Barsbold, 1983a; IGM 100/20, IGM 100/21; IGM 100/22; IGM 100/23)
Albertosaurus sarcophagus (Currie, 2003)
Albinykus bataar (Nesbitt et al., 2011; IGM 100/3004)
Allosaurus fragilis (Madsen, 1976; AMNH FR 257, AMNH FR 275, AMNH FR 281, AMNH FR 287, AMNH FR 290, UMNH VP 16605, UMNH 16652, UUVP 5961)
Alvarezsaurus calvoi (Bonaparte, 1991; MUCPv 54)
Alxasaurus elesitaiensis (Russell and Dong, 1993; Clark et al., 2004)
Anas platyrhynchus (AMNH 27496)
Anchiornis huxleyi (Xu et al., 2009; Hu et al., 2009)
Anserimimus planinychus (Barsbold, 1988)
Apsaravis ukhaana (Norell and Clarke, 2001; Clarke and Norell, 2002; IGM 100/1017)
Archaeornithomimus asiaticus (Gilmore, 1933; Makovicky et al., 2004; AMNH FR 6558, AMNH FR 6565, AMNH FR 6566, AMNH FR 6567, AMNH FR 6568, AMNH FR 6569, AMNH FR 6570, AMNH FR 21626, AMNH FR 21627, AMNH FR 21786, AMNH FR 21787, AMNH FR 21788, AMNH FR 21789, AMNH FR 21790, AMNH FR 21791, AMNH FR 21797, AMNH FR 21896, AMNH FR 21802)
Archaeopteryx lithographica (de Beer, 1954; Ostrom, 1976b; Wellnhofer, 1974, 1993; Mayr et al., 2005; Norell et al., 2001; BMNH 37001)
Atrociraptor marshalli (Currie and Varricchio, 2004)
Austroraptor cabazai (Novas et al., 2009; MML–195)
Avimimus portentosus (Kurzanov, 1981; Vickers-Rich et al., 2002; Osmólska et al., 2004)
Balaur bondoc (Csiki et al., 2010; EME PV.313; FGGUB R.1580–R.1585)
Bambiraptor feinbergorum (Burnham et al., 2000; AMNH FR 30556)
Baptornis advenus (Marsh, 1877a; AMNH FR 5101)
Buitreraptor gonzalezorum (Makovicky et al., 2005; MPCA-PV 245, MPCA-PV 238)
Byronosaurus jaffei (Norell et al., 2001; Makovicky et al., 2003; IGM 100/983, IGM 100/984)
Cathayornis yandica (Zhou et al., 1992; Zhou, 1995; Zhou and Hou, 2002; Hou, 1997)
Caudipteryx zoui (Ji et al., 1998; NGMC 97-9-A)
Chauna torquata (AMNH 3617)
Chirostenotes pergracilis (Currie and Russell, 1988; Sues, 1997; Osmólska et al., 2004)
Citipati osmolskae (Clark et al., 2001, 2002; IGM 100/978, IGM 100/979)
Coelurus fragilis (YPM 2010)
Compsognathus longipes (Bidar et al., 1972; Ostrom, 1978; Gishlick and Gauthier, 2007; Peyer, 2006; MNHN CNJ 79)
Conchoraptor gracilis (Barsbold, 1981, 1986a, 1986b; Kundrát and Janácek, 2007; IGM uncataloged)
Concornis lacustris (Sanz et al., 1993, 1995)
Confuciusornis sanctus (Chiappe et al., 1999; GMV 2131, IVPP V11370, IVPP V11374, IVPP V11375, IVPP V13171, IVPP V14385)
Crax yubra (AMNH 6272)
Crypturellus undullatus (AMNH 2751)
Daspletosaurus torsus (Russell, 1970; Currie, 2003)
Deinonychus antirrhopus (Maxwell and Witmer, 1996; Brinkman et al., 1998; Ostrom, 1969a, 1969b, 1974, 1976a; YPM 5240, YPM 5205, AMNH FR 3015)
Dilong paradoxus (Xu et al., 2004; IVPP V14242, IVPP V14243, IVPP V11579)
Dromaeosaurus albertensis (Currie, 1995; AMNH FR 5356)
Epidendrosaurus ningchengensis (Zhang et al., 2002)
Epidexipteryx hui (Zhang et al., 2008)
Erlikosaurus andrewsi (Perle, 1981; Clark et al., 1994, 2004; IGM 100/111)
Eotyrannus lengi (Hutt et al., 2001; MIWG 1997.550)
Gallimimus bullatus (Osmólska et al., 1972; Makovicky et al., 2004; Makovicky and Norell, 1988; IGM 100/1133)
Gallus gallus (AMNH 27820)
Garudimimus brevipes (Barsbold, 1981; Kobayashi and Barsbold, 2005)
Gobipteryx minuta (Elżanowski, 1976; Chiappe et al., 2001)
Gorgosaurus libratus (Norell et al., 2001; Currie, 2003; Russell, 1970; Lambe, 1914a, 1914b, 1917)
Graciliraptor lujiatunensis (Xu and Wang, 2004; IVPP V13474)
Haplocheirus sollers (Choiniere et al., 2010)
Harpymimus okladnikovi (Barsbold and Perle, 1984; Makovicky et al., 2004; Kobayashi and Barsbold, 2005)
Hesperonychus elizabethae (Longrich and Currie, 2009)
Hesperornis regalis (Marsh, 1880)
Hongshanornis longicresta (Zhou and Zhang, 2005; IVPP V14533)
Huaxiagnathus orientalis (Hwang et al., 2004b; CAGS-IG02-301)
Iaceornis marshi (Clarke, 2004)
Ichthyornis dispar (Marsh, 1872, 1880; Clarke, 2004)
Incisivosaurus gauthieri (Xu et al., 2002b; IVPP V13326)
Ingenia yanshani (IGM 100/973)
Jeholornis prima (Ji et al., 2002a, 2003b; Zhou and Zhang, 2002a, 2003a; IVPP V13353, IVPP V13274)
Jinfengopteryx elegans (Ji et al., 2005)
Jixiangornis orientalis (Ji et al., 2002b; CAGS uncataloged)
Juravenator starki (Gohlich and Chiappe, 2006; JME 200)
Limenavis patagonicus (Clarke and Chiappe, 2001)
Liaoningornis longidigitris (Hou, 1996; Hou, 1997; Zhou and Hou, 2002)
Lithornis sp: (Houde, 1988; AMNH 21900, AMNH 21901, AMNH 21902, AMNH 21903)
Mahakala omnogovae (Turner et al., 2007b; IGM 100/1033)
Mei long (Xu and Norell, 2004; IVPP V12733)

Microraptor zhaoianus (Xu et al., 2000; Hwang et al., 2002; BPM 1 3-13; IVPP V12330, IVPP V12727, IVPP V13320, IVPP V13476, uncataloged 1, uncataloged 2, uncataloged 3)
Microraptor "gui" (Xu et al., 2003; IVPP V13352)
Microvenator celer (Makovicky and Sues, 1998; AMNH FR 3041)
Mononykus olecranus (Perle et al., 1993, 1994; Chiappe et al., 2002; IGM 107/6)
Neuquenraptor argentinus (Novas and Pol, 2005; MCF PVPH-77)
Neuquenraptor sp. (MUCPv uncataloged)
Neuquenornis volans (Chiappe and Calvo, 1994; MUCPv 142)
Ornitholestes hermanni (Osborn, 1903, 1917; AMNH FR 619, AMNH FR 587)
Ornithomimus edmontonicus (Parks, 1926, 1928; Ma kovicky et al., 2004; AMNH FR 5201)
Oviraptor philoceratops (Osborn, 1924b; AMNH FR 6517)
Patagonykus puertai (Novas, 1997; MCF PVPH-37)
Patagopteryx deferrariisi (Chiappe, 2004; MACN N 11, MUCPv 48, MUCPv 207)
Pedopenna daohugouensis (Xu and Zhang, 2005)
Pelecanimimus polydon (Pérez-Moreno et al., 1994; Makovicky et al., 2004)
Pengornis houi (Zhou et al., 2008)
Proceratosaurus bradleyi (von Huene, 1926; BMNH R4860)
Pyroraptor olympius (Allain and Taquet, 2000; MNHN BO 001, MNHN BO 002, MNHN BO 003, MNHN BO 004, MNHN BO 005, MNHN BO 006, MNHN BO 007, MNHN BO 008, MNHN BO 009, MNHN BO 010, MNHN BO 012, MNHN BO 017, MNHN BO uncataloged)
Rahonavis ostromi (Forster et al., 1998; UA 8656)
Rinchenia mongoliensis (Barsbold, 1986; Osmólska et al., 2004)
Sapeornis chaoyangensis (Zhou and Zhang, 2002b, 2003b; IVPP V13396, IVPP V15488)
Saurornithoides mongoliensis (Osborn, 1924b; Mako vicky and Norell, 2004; Norell et al., 2009; AMNH FR 6515)
Saurornitholestes langstoni (Sues, 1978; Norell et al., 2001; MOR 660; TMP 67.20.36; TMP 88.121.39; TMP 64.10.5)
Segnosaurus galbinensis (Perle, 1979, 1981; Clark et al., 2004)
Shanag ashile (Turner et al., 2007a; IGM 100/1119)
Shenzhousaurus orientalis (Ji et al., 2003a; NGMC 97-4-002)
Shuvuuia deserti (Chiappe et al., 1998a, 2002; Suzuki et al., 2002; IGM 100/975, IGM 100/977, IGM 100/1001, IGM 100/1276, IGM 100/1304, IGM 100/1827, MPD 100/120)
Sinornithoides youngi (Russell and Dong, 1993; Currie and Dong, 2001; IVPP V9612)
Sinornithosaurus millenii (Xu et al., 1999; Xu and Wu, 2001)
Sinraptor dongi (Currie and Zhao, 1993)
Sinosauropteryx prima (Ji and Ji, 1996; Currie and Chen, 2001)
Sinovenator changii (Xu et al., 2002a; IVPP V9612)
Songlingornis linghensis (Hou, 1997)
Struthiomimus altus (Osborn, 1917; Makovicky et al., 2004; AMNH FR 5339, AMNH FR 5257)
Tarbosaurus bataar (Currie, 2003; IGM unnumbered?)
Tianyuraptor ostromi (Zheng et al., 2010)
Troodon formosus (Currie, 1985; Currie and Zhao, 1993; Norell et al., 2001; Makovicky et al., 2003)
Tsaagan mangas (Norell et al., 2006; IGM 100/1015)
Tyrannosaurus rex (Brochu, 2003; Currie, 2003; AMNH FR 5027; FMNH PR 2081)
Undescribed troodontid 1 ("EK Troodontid" IGM 100/44)
Undescribed troodontid 2 (IGM 100/1126)
Undescribed troodontid 3 (IGM 100/1323)
Unenlagia comahuensis (Novas and Puerta, 1997; Novas, 2004; MCF PVPH-78)
Unenlagia paynemili (Calvo et al., 2004; MUCPv 343, 349, 409, 415, 416)
Utahraptor ostrommaysorum (Kirkland et al., 1993; Britt et al., 2001; CEU 184v.400/CEUM 1430, CEU 184v.86/CEUM 1456, CEU 184v.42/CEUM 1112, CEU 184v.1145/CEUM 39596, CEU 184v.300/CEUM 1370, CEU 184v.215/CEUM 1285, CEU 184v.457/CEUM 4023, CEU 184v.1010/CEUM 5440, CEU 184v.667/CEUM 3538, CEU 184v.1072/CEUM 8586, CEU 184v.180/CEUM 1250, CEU 184v.260/CEUM 1330, CEU 184v.792/CEUM 3666, CEU 184v.951/CEUM 5372, CEU 184v.883/CEUM 3928, BYU VP 14569, BYU VP 14614, BYU VP uncataloged premaxilla, BYU VP uncataloged coracoid—field number 3269, BYU VP 14389, BYU VP 14024, BYU VP 15634, BYU VP 14627, BYU VP 9941, BYU VP 15209, BYU VP 18118, BYU VP 11056, BYU VP 14287, BYU VP 18085, BYU VP 11300, BYU VP 18086, BYU VP 18049, BYU VP 18073, BYU VP 9438, BYU VP 14701, BYU VP 15484, BYU VP 14146, BYU VP 18048, BYU VP 18087, BYU VP 15690, BYU VP 15465, BYU VP 14281, BYU VP 15417, BYU VP 18079, BYU VP 15416, BYU VP 14567, BYU VP 10748, BYU VP 14500, BYU VP 14776, BYU VP 15204, BYU VP 14372)
Velociraptor mongoliensis (Barsbold and Osmolska, 1999; AMNH FR 6515, IGM 100/24, IGM 100/25, IGM 100/976, IGM 100/982, IGM 100/985, PIN 3143/8, ZPAL MgD-8/97)
Vorona berivotrensis (Forster et al., 1996, 2002; UA 8651, FMNH PA 715, FMNH PA 717)
Xixiasaurus henanensis (Lü et al., 2010)
Xiaotingia zhengi (Xu et al., 2011)
Yanornis martini (Zhou and Zhang, 2001; IVPP V12444)
Yixianornis grabaui (Clarke et al., 2006; Zhou and Zhang, 2001; IVPP V12631)
Zanabazar junior (Barsbold, 1974; Makovicky and Norell, 2004; Norell et al., 2009; IGM 100/1)

APPENDIX 2

Character List

The complete list of characters and scores are available on on Morphobank (O'Leary and Kaufman, 2007) online (http://www.morphobank.org or at http://morphobank.org/permalink/?660).

Characters 6, 50, and 52 should be excluded during analysis as newly added characters now subsume them. The remaining 474 characters were used in the phylogenetic analysis. Characters 16, 17, 18, 27, 40, 68, 76, 110, 113, 125, 132, 157, 169, 174, 198, 200, 235, 265, 266, 269, 272, 284, 292, 314, 321, 324, 326, 331, 333, 356, 364, 369, 384, 390, 392, 398, 402, 406, 414, 418, 420, 422, 425, 430, 431, 432, 433, 438, 448, and 450 were ordered because they either represent potentially nested statements of primary homology or include presence/absence states. TWiG = Theropod Working Group; CEA 06 = Clarke et al. (2006); MAE 05 = Makovicky et al. (2005).

Character 1: Vaned feathers on forelimb

0: symmetric

1: asymmetric

The barbs on opposite sides of the rachis differ in length; in extant birds, the barbs on the leading edge of flight feathers are shorter than those on the trailing edge. *Sinosauropteryx prima*, *Caudipteryx zoui*, and *Sinornithosaurus millenii* are state 0. The derived state is present in *Microraptor zhaoianus and Archaeopteryx lithographica*, *Confuciusornis sanctus,* and all avialans that preserve integumentary structures. The derived state is synapomorphic for Avialae and autapomorphic for *Microraptor zhaoianus*.

Character 2: Orbit shape

0: round in lateral or dorsolateral view

1: dorsoventrally elongate

It is improbable that the eye occupied the entire orbit of those taxa in which it is keyhole shaped. Only *Allosaurus fragilis*, *Sinraptor dongi*, *Tyrannosaurus rex,* and *Albertosaurus sarcophagus* have the derived, dorsoventrally elongate orbit (state 1).

Character 3: Anterior process of postorbital

0: projects into orbit

1: does not project into orbit

In the current context, an anterior process of the postorbital that projects into the orbit (state 0) is synapomorphic for tyrannosaurids. The feature however is not present in *Dilong paradoxus*.

Character 4: Postorbital in lateral view

0: with straight anterior (frontal) process

1: frontal process curves anterodorsally and dorsal border of temporal bar is dorsally concave

The derived state appears to be present in all maniraptorans that preserve a postorbital. Ornithomimosaurs, derived tyrannosaurs and *Ornitholestes hermanni* possess the primitive straight anterior process on the postorbital, as do *Allosaurus fragilis* and *Sinraptor dongi*. Complicating this distribution, however, is the presence of the derived condition in the alvarezsaurid *Shuvuuia deserti*, although it is unknown in *Patagonykus puertai* and *Alvarezsaurus calvoi*.

Character 5: Postorbital bar

0: parallels quadrate, lower temporal fenestra rectangular in shape

1: jugal and postorbital approach or contact quadratojugal to constrict lower temporal fenestra

The derived state for this character is synapomorphic for a derived clade of Ornithomimosaurs including *Struthiomimus altus*, *Gallimimus bullatus*, and *Ornithomimus edmonticus*. However, this character is unknown for other Ornithomimosaurs and therefore may be present more broadly in the group.

EXCLUDED Character 6: Otosphenoidal crest position

0: vertical on basisphenoid and prootic, and does not border an enlarged pneumatic recess

1: well developed, crescent shaped, thin crest forms anterior edge of enlarged pneumatic recess

This structure forms the anterior, and most distinct, border of the "lateral depression" of the middle ear region (Currie, 1985; Currie and Zhao, 1993) of derived troodontids and some extant avians. A well-developed crescent-shaped otosphenoidal crest forming the anterior edge of an enlarged pneumatic recess is present in Chirostenotes gracilis, Shuvuuia deserti *(unknown in other alvarezsaurs),* Troodon formosus, Saurornithoides mongoliensis *and* Saurornithoides junior, Byronosaurus jaffei, *and* Sinornithoides youngi. *It is not present in the basal troodontids* Mei long *and* Sinovenator changii.

This character is excluded in favor of character 468.

Character 7: Crista interfenestralis location

0: confluent with lateral surface of prootic and opisthotic

1: distinctly depressed within middle ear opening

The distribution of character states for this character is poorly known. Only 11 taxa (~24%) can be coded for this character. *Mononykus olecranus*, *Shuvuuia deserti, Archaeopteryx lithographica, Byronosaurus jaffei, Sinovenator changii* and the Early Cretaceous troodontid IGM 100/44 possess a crista interfenestralis confluent with the lateral surface of the prootic and opisthotic (state 0). *Troodon formosus*, *Tsaagan mangas*, *Velociraptor mongoliensis*, *Dromaeosaurus albertensis,* and *Citipati osmolskae* exhibit a distinctly depressed crista interfenestralis (state 1). Currently the character distribution within the outgroup is unknown.

Character 8: Subotic recess (pneumatic fossa ventral to fenestra ovalis)

0: absent

1: present

A subotic recess is primitive absent in theropods. *Struthiomimus altus*, *Gallimimus bullatus*, *Ornithomimus edmonticus*, *Troodon formosus*, *Saurornithoides mongoliensis*, *Saurornithoides junior*, *Byronosaurus jaffei*, and the Early Cretaceous troodontid IGM 100/44 possess a subotic recess. This was used by some authors to suggest a sister-group relationship between troodontids and ornithomimosaurs. It is clear that the structures in the two groups are convergent given that basal troodontids such as *Sinovenator changii* lack a subotic recess.

Character 9: Basisphenoid recess

0: present between basisphenoid and basioccipital

1: entirely within basisphenoid

2: absent

A basisphenoid recess appears to be absent only in troodontids (e.g., *Troodon formosus, Saurornithoides junior*, *Sinovenator changii*, and EK troodontid IGM 100/44) and the therizinosaur *Erlikosaurus andrewsi* (although it is unknown in *Segnosaurus galbinensis* and *Alxasaurus elesitaiensis*). The outgroup exhibits state 0—a recess present between the basioccipital and basisphenoid. State 0 is also present in the tyrannosauroids *Dilong paradoxus* and *Albertosaurus libratus*,

the oviraptorosaurs *Citipati osmolskae* and *Chirostenotes pergracilis*, the dromaeosaurids *Tsaagan mangas, Velociraptor mongoliensis*, and *Dromaeosaurus albertensis*, the alvarezsaurid *Shuvuuia deserti*, and in *Ornitholestes hermanni*. Therefore, it appears that state 0 is the primitive condition for coelurosaurs and that a basisphenoid recess entirely within the basisphenoid was independently derived at least twice within coelurosaurs—once in oviraptorosaurs (e.g., *Incisivosaurus gauthieri*, *Avimimus portentosus*, *Struthiomimus altus*, *Gallimimus bullatus*, and *Ornithomimus edmonticus*) and once in *Tyrannosaurus rex*. Complicating understanding the distribution of this character is the lack of data for compsognathids and limited sampling in tyrannosaurids. For instance, with *Albertosaurus libratus* and *Dilong paradoxus* both showing state 0, it is unclear whether state 1 is autapomorphic for *Tyrannosaurus rex* or it diagnoses a more restricted clade of tyrannosaurids.

Character 10: Posterior opening of basisphenoid recess

0: single

1: divided into two small, circular foramina by a thin bar of bone

A posteriorly divided basisphenoid recess is present in *Citipati osmolskae*, *Chirostenotes pergracilis*, the dromaeosaurids *Tsaagan mangas*, *Deinonychus antirrhopus*, and *Velociraptor mongoliensis*, and the tyrannosauroid *Tyrannosaurus rex*.

Character 11: Base of cultriform process (parasphenoid rostrum)

0: not highly pneumatized

1: expanded and pneumatic (parasphenoid bulla present)

A parasphenoid bulla is present in all ornithomimosaurs that have braincases preserved (e.g., *Gallimimus bullatus*, *Garudimimus brevipes*, and *Pelecanimimus polydon*) as well as in the troodontids *Troodon formosus*, *Saurornithoides mongoliensis*, and *Saurornithoides junior*. This was used by some authors to suggest a sister-group relationship between troodontids and ornithomimosaurs. However, the absence of a parasphenoid bulla in the basal troodontid demonstrates that the character evolved independently in troodontids.

Character 12: Basipterygoid processes project (modified from TWiG char. 12)

0: ventral or anteroventrally projecting

1: lateroventrally projecting

2: laterally

Lateroventrally projecting basipterygoid processes are known in *Avimimus portentosus*, the ornithomimosaurs *Gallimimus bullatus*, *Garudimimus brevipes*, and *Ornithomimus edmonticus*, and in the derived troodontids *Troodon formosus*, *Saurornithoides mongoliensis*, *Saurornithoides junior*, and *Byronosaurus jaffei*. A third state was added to score the condition present in derived avialans.

Character 13: Basipterygoid processes

0: well developed, extending as a distinct process from the base of the basisphenoid

1: processes abbreviated or absent (1).

Abbreviated basipterygoid processes (state 1) are present in oviraptorosaurs (e.g., *Citipati osmolskae*, *Oviraptor philoceratops*, *Incisivosaurus gauthieri*, *Chirostenotes pergracilis*, and *Avimimus portentosus*) and in the therizinosaur *Erlikosaurus andrewsi*; however, this character is unknown in *Alxasaurus elesitaiensis*.

Character 14: Basipterygoid processes

0: solid

1: processes hollow

Hollow basipterygoid processes (state 1) are present in *Chirostenotes pergracilis*, the ornithomimosaurs *Gallimimus bullatus*, *Garudimimus brevipes*, and *Ornithomimus edmonticus*, as well as in the derived troodontids *Troodon formosus, Saurornithoides mongoliensis, Saurornithoides junior, and Byronosaurus jaffei.*

Character 15: Basipterygoid recesses on dorsolateral surfaces of basipterygoid processes

0: absent

1: present

Character 16: Depression for pneumatic recess on prootic (dorsal tympanic recess) ORDERED

0: absent

1: present as dorsally open fossa on prootic/opisthotic

2: present as deep, posterolaterally directed concavity

The dorsal tympanic recess referred to here is the depression anterodorsal to the middle ear on the opisthotic, not the recess dorsal to the crista interfenestralis within the middle ear as seen in *Archaeopteryx lithographica, Shuvuuia deserti,* and Aves.

Character 17: Accessory tympanic recess dorsal to crista interfenestralis ORDERED

0: absent

1: small pocket present

2: extensive with indirect pneumatization

According to Witmer (1990), this structure may be an extension from the caudal tympanic recess, although it has been interpreted as the main part of the caudal tympanic recess by some previous authors. A small pocket (state 1) is located dorsal to the crista interfenestralis in *Mononykus olecranus*, *Shuvuuia deserti*, *Archaeopteryx lithographica*, *Byronosaurus jaffei*, and *Sinovenator changii*. *Citipati osmolskae* shows state 2, extensive indirect pneumatization. An accessory recess is known to be absent in *Allosaurus fragilis, Sinraptor dongi, Dromaeosaurus albertensis, Velociraptor mongoliensis, Tsaagan mangas, Struthiomimus altus, Gallimimus bullatus, Ornithomimus edmonticus, Tyrannosaurus rex, and Troodon formosus.*

Character 18: Caudal (posterior) tympanic recess ORDERED

0: absent

1: present as opening on anterior surface of paroccipital process

2: extends into opisthotic posterodorsal to fenestra ovalis, confluent with this fenestra

Character 19: Exits of cranial nerves X–XII

0: flush with surface of exoccipital

1: located together in a bowllike depression

Character 20: Maxillary process of premaxilla

0: contacts nasal to form posterior border of nares

1: reduced so that maxilla participates broadly in external naris

2: extends posteriorly to separate maxilla from nasal posterior to nares

Character 21: Internarial bar shape

0: rounded
1: flat

Character 22: Crenulated margin on buccal edge of premaxilla
0: absent
1: present

Character 23: Position of caudal margin of naris (Chiappe et al., 1998b)
0: farther rostral than the rostral border of the antorbital fossa
1: nearly reaching or overlapping the rostral border of the antorbital fossa

Character 24: Premaxillary symphysis shape
0: acute, V-shaped
1: rounded, U-shaped

Character 25: Secondary palate (redefined by MAE 05)
0: short
1: long, with extensive palatal shelves on maxilla

Character 26: Palatal shelf of maxilla
0: flat
1: with midline ventral "toothlike" projection

Character 27: Pronounced, round accessory antorbital fenestra (modified from TWiG) ORDERED
0: absent
1: present, fenestra occupies less than half of the depressed area between the anterior margins of the antorbital fossa and antorbital fenestra
2: present, fenestra large and takes up most of the space between the anterior margins of the antorbital fenestra and fossa

A small fenestra, variously termed the *accessory antorbital fenestra* or *maxillary fenestra,* penetrates the medial wall of the antorbital fossa anterior to the antorbital fenestra in a variety of coelurosaurs and other theropods. This character was modified from the TWiG character following Currie and Varricchio (2004: char. 22).

Character 28: Accessory antorbital fossa
0: situated at rostral border of antorbital fossa
1: situated posterior to rostral border of fossa

Character 29: Tertiary antorbital fenestra (fenestra promaxillaris)
0: absent
1: present

Character 30: Narial region
0: apneumatic or poorly pneumatized (0)
1: with extensive pneumatic fossae, especially along posterodorsal rim of naris

Character 31: Jugal and postorbital
0: both contribute equally to postorbital bar
1: ascending process of jugal reduced and descending process of postorbital ventrally elongate

Character 32: Jugal height beneath lower temporal fenestra
0: tall, twice or more as tall dorsoventrally as it is wide transversely
1: rodlike

Character 33: Jugal, pneumatic recess in posteroventral corner of antorbital fossa
0: present
1: absent

Character 34: Medial jugal foramen
0: present on medial surface ventral to postorbital bar
1: absent

Character 35: Quadratojugal shape
0: without horizontal process posterior to ascending process (reversed L shape)
1: with process (i.e., inverted T or Y shape)

Character 36: Jugal and quadratojugal
0: separate
1: quadratojugal and jugal fused and not distinguishable from one another

Character 37: Supraorbital crests on lacrimal in adult individuals
0: absent
1: dorsal crest above orbit
2: lateral expansion anterior and dorsal to orbit

Supraorbital crests are variably present within Theropoda, and is present in immediate coelurosaur outgroups such as *Allosaurus* and *Sinraptor*. Among coelurosaurs that are primarily found among basal members such as tyrannosauroids like *Dilong*, *Eotyrannus*, and derived tyrannosaurids like *Daspletosaurus* and *Tyrannosaurus*. An unambiguous synapomorphy of all troodontids examined is the third state of this character; a large lateral expansion anterior and dorsal to the orbit. This expansion in troodontids takes the form of a large triangular lamina. The small angle of the triangle is present anterior to the preorbital bar whereas the widest portion of the crest is posteriorly above the anterior margin of the orbit. Dorsoventrally this crest is very thin and originates from the very dorsalmost surface of the lacrimal.

Character 38: Enlarged foramen or foramina opening laterally at the angle of the lacrimal above antorbital fenestra
0: absent
1: present

Character 39: Lacrimal anterodorsal process
0: absent (inverted L shaped)
1: T-shaped in lateral view
2: anterodorsal process much longer than posterior process

Character 40: Prefrontal ORDERED
0: large, dorsal exposure similar to that of lacrimal
1: greatly reduced in size
2: absent

Character 41: Frontals
0: narrow anteriorly as a wedge between nasals
1: end abruptly anteriorly, suture with nasal transversely oriented

Character 42: Anterior emargination of supratemporal fossa on frontal (Currie, 1995)
0: straight or slightly curved
1: strongly sinusoidal and reaching onto postorbital process (1)

Character 43: Frontal postorbital process (dorsal view) (Currie, 1995)
0: smooth transition from orbital margin
1: sharply demarcated from orbital margin

Character 44: Frontal edge (Currie, 1995)
0: smooth in region of lacrimal suture
1: edge notched

Character 45: Dorsal surface of parietals
0: flat, lateral ridge borders supratemporal fenestra
1: parietals dorsally convex with very low sagittal crest along midline
2: dorsally convex with well-developed sagittal crest

Character 46: Parietals

0: separate
1: fused

Character 47: Descending process of squamosal
0: parallels quadrate shaft
1: lies nearly perpendicular to quadrate shaft

Character 48: Descending process of squamosal
0: contacts quadratojugal
1: does not contact quadratojugal

Character 49: Posterolateral shelf on squamosal overhanging quadrate head (Currie, 1995)
0: absent
1: present

EXCLUDED Character 50: Dorsal process of quadrate
0: single headed
1: with two distinct heads, a lateral one contacting the squamosal and a medial head contacting the braincase
This character was excluded in favor of two separate characters that seems to more clearly and explicitly capture the morphology described by character 50. That is, this splitting of the character serves to distinguish a single- or double-headed quadrate and whether or not it articulates with the squamosal only or with the lateral braincase wall as well. As taxon sampling has become more dense within paravians it is now apparent that these two states are not codependent. Characters 296 and 297 replace this character.

Character 51: Quadrate orientation
0: vertical
1: strongly inclined anteroventrally so that distal end lies far forward of proximal end

EXCLUDED Character 52: Quadrate (Molnar, 1985)
0: solid
1: hollow, with foramen on posterior surface
This character was excluded in favor of characters 299, 300, and 301, which capture a much wider range of morphologies associated with quadrate pneumaticity.

Character 53: Lateral border of quadrate shaft (Currie, 1995)
0: straight
1: with broad, triangular process along lateral edge of shaft contacting squamosal and quadratojugal above an enlarged quadrate foramen

Character 54: Foramen magnum shape (Makovicky and Sues, 1998)
0: subcircular, slightly wider than tall
1: oval, taller than wide

Character 55: Occipital condyle
0: without constricted neck
1: subspherical with constricted neck

Character 56: Paroccipital process
0: elongate and slender, with dorsal and ventral edges nearly parallel
1: process short, deep with convex distal end

Character 57: Paroccipital process
0: straight, projects laterally or posterolaterally
1: distal end curves ventrally, pendant

Character 58: Paroccipital process (Currie, 1995)
0: with straight dorsal edge
1: with dorsal edge twisted rostrolaterally at distal end

Character 59: Ectopterygoid
0: with constricted opening into ventral fossa
1: with open ventral fossa in the main body of the element

Character 60: Dorsal recess on ectopterygoid
0: absent
1: present

Character 61: Flange of pterygoid
0: well developed
1: reduced in size or absent

A reduced or absent pterygoid flange occurs in a number of coelurosaur groups. Avialans including *Archaeopteryx* have a reduced or absent flange as do the therizinosauroid *Erlikosaurus andrewsi*, the alvarezsaurid *Shuvuuia deserti,* and all oviraptorosaurs in which the flange can be observed (e.g., *Citipati osmolskae*, *Oviraptor philoceratops*, *Incisivosaurus gauthieri*).

Character 62: Palatine and ectopterygoid (Currie, 1995)
0: separated by pterygoid
1: contact

Character 63: Palatine shape (Elzanowski and Wellnhofer, 1996)
0: tetraradiate, with jugal process
1: palatine triradiate, jugal process absent

Character 64: Suborbital fenestra (Clark et al., 1994)
0: similar in length to orbit
1: reduced in size (less than one-quarter orbital length) or absent

Character 65: Symphyseal region of dentary
0: broad and straight, paralleling lateral margin
1: medially recurved slightly
2: strongly recurved medially

Character 66: Dentary symphyseal region
0: in line with main part of buccal edge
1: symphyseal end downturned

Character 67: Mandible
0: without coronoid prominence
1: with coronoid prominence

Character 68: Posterior end of dentary ORDERED
0: without posterodorsal process dorsal to mandibular fenestra
1: with dorsal process above anterior end of mandibular fenestra
2: with elongate dorsal process extending over most of fenestra

Character 69: Labial face of dentary (Russell and Dong, 1993)
0: flat
1: with lateral ridge and inset tooth row

Character 70: Dentary shape (Currie, 1995)
0: subtriangular in lateral view
1: with subparallel dorsal and ventral edges

Character 71: Nutrient foramina on external surface of dentary (Currie, 1987)
0: superficial
1: lying within deep groove

Character 72: External mandibular fenestra shape
0: oval
1: subdivided by a spinous rostral process of the surangular

This is a derived oviraptorid synapomorphy present in *Conchoraptor gracilis*, *Oviraptor philoceratops*, *Citipati osmolskae*, and *Ingenia yanshani*.

Character 73: Internal mandibular fenestra (Currie, 1995)
0: small and slitlike
1: large and rounded

Character 74: Foramen in lateral surface of surangular rostral to mandibular articulation
0: absent
1: present
Character 75: Splenial
0: not widely exposed on lateral surface of mandible
1: exposed as a broad triangle between dentary and angular on lateral surface of mandible
Character 76: Coronoid ossification ORDERED
0: large
1: only a thin splint
2: absent
Character 77: Articular
0: without elongate, slender medial, posteromedial, or mediodorsal process from retroarticular process
1: with process
Character 78: Retroarticular process
0: short, stout
1: elongate and slender
Character 79: Mandibular articulation surface
0: as long as distal end of quadrate
1: twice or more as long as quadrate surface, allowing anteroposterior movement of mandible
Character 80: Premaxilla
0: toothed
1: edentulous
Character 81: Second premaxillary tooth (Currie, 1995)
0: approximately equivalent in size to other premaxillary teeth
1: second tooth markedly larger than third and fourth premaxillary teeth
Character 82: Maxilla
0: toothed
1: edentulous
Character 83: Maxillary and dentary teeth
0: serrated
1: some without serrations anteriorly (except at base in *S. mongoliensis*)
2: all without serrations
Character 84: Dentary and maxillary teeth
0: large
1: small (25–30 in dentary)
Character 85: Dentary teeth (Currie, 1987)
0: in separate alveoli
1: set in open groove
Character 86: Serration denticles (Farlow et al., 1991, quantify this difference)
0: large
1: small
Character 87: Serrations
0: simple, denticles convex
1: distal and often mesial edges of teeth with large, hooked denticles that point toward the tip of the crown
Character 88: Teeth
0: constricted between root and crown
1: root and crown confluent
Character 89: Dentary teeth
0: evenly spaced
1: anterior dentary teeth smaller, more numerous, and more closely appressed than those in middle of tooth row
Character 90: Dentaries
0: lack distinct interdental plates
1: with interdental plates medially between teeth (1).

Currie (1995) suggests the interdental plates of dromaeosaurids are present but fused to the medial surface of the dentary, whereas they are absent in troodontids. In the absence of a definitive, nondestructive method for parsing between fusion/loss we do not recognize this distinction, and code all taxa that lack distinct interdental plates with state 1.

Character 91: In cross section, premaxillary tooth crowns
0: suboval to subcircular
1: asymmetrical (D-shaped in cross section) with flat lingual surface
Character 92: Number of cervical vertebrae
0: ≤10 (0)
1: 12 or more
Character 93: Axial epipophyses
0: absent or poorly developed, not extending past posterior rim of postzygapophyses
1: large and posteriorly directed, extend beyond postzygapophyses

This character is modified from Gauthier's (1986) character 69 and Makovicky and Sues's (1998) character 30. Rauhut's (2003) character 92 also pertains to axial epipophyseal morphology. Rauhut (2003) has a three-state ordered character describing the epiphyses on the axis as absent, present as a small ridge, or present and strongly pronounced, overhanging the postzygapophyses. Rauhut (2003) considers *Herrerasaurus*, *Monolophosaurus*, *Microvenator*, *Avimimus*, and Ornithomimosauria as possessing small ridgelike epipophyses (state 1). Large and posteriorly directed epipophyses that extend beyond the postzygapophysis are present in *Allosaurus fragilis* and *Sinraptor dongi*. This character is reversed (state 0) at the base of all Coelurosauria more derived than Tyrannosauroidea. In more derived coelurosaurs, large epipophyses extending beyond the postzygapophyses is recovered as a paravian synapomorphy although it is reversed (state 0) in troodontids more derived than *Sinovenator changii* + *Mei long*. This optimization is based on the presence of state 0 in EK troodontid and *Byronosaurus jaffei*. The condition is unknown in *Troodon*, *Saurornithoides*, and *Sinornithoides*.

Character 94: Axial neural spine
0: flared transversely
1: compressed mediolaterally

A mediolaterally compressed axial neural spine is present in all coelurosaurs for which this element is known except *Tyrannosaurus rex*, *Albertosaurus libratus*, and *Archaeornithomimus asiaticus*. The spine is flared transversely in these taxa as well as in the outgroups *Allosaurus* and *Sinraptor*.

Character 95: Epipophyses of cervical vertebrae
0: placed distally on postzygapophyses, above postzygapophyseal facets
1: placed proximally, proximal to postzygapophyseal facets

As currently scored, only seven taxa (*Shuvuuia deserti*, *Microvenator celer*, *Avimimus portentous*, *Gallimimus bullatus*, *Troodon formosus*, *Sinovenator changii*, and *Citipati osmolskae*) are known to possess a proximally placed epipophysis (state 1). However,

given the distribution across the tree it is now most parsimonious to interpret this character state as synapomorphic for all coelurosaurs more derived than *Tyrannosaurus rex* + *Albertosaurus libratus*. The character is refered to the more widespread theropod condition (state 0; distally placed above the post-zygapophyses) in Compsognathids, dromaeosaurids, and *Mei long*.

Character 96: Anterior cervical centra

0: level with or shorter than posterior extent of neural arch

1: centra extending beyond posterior limit of neural arch

In most basal theropods (e.g., *Coelophysis*, *Dilophosaurus* (UCMP 37302) *Allosaurus fragilis*, *Tyrannosaurus rex* (FMNH PR2081), the anterior cervical centra does not extent beyond the posterior limit of the neural arch. An anterior cervical centra that extends beyond the posterior limit of the neural arch (state 1) is synapomorphic for all coelurosaurs more derived than Tyrannosauroidea. A reversal to anterior cervical centra that are level or shorter than the posterior extent of the neural arch (state 0) is present in *Avimimus portentosus* and is synapomorphic for Dromaeosauridae (known in *Microraptor zhaoianus*, *Tsaagan mangas*, *Saurornitholestes langstoni*, *Velociraptor mongoliensis*, and *Deinonychus antirrhopus*).

Character 97: Carotid process on posterior cervical vertebrae

0: absent

1: present

This is a very "avian" characteristic. Carotid processes are present in *Buitreraptor gonzalezorum*, *Mei long*, *Sinornithoides youngi*, *Troodon formosus*, *Avimimus portentosus*, *Shuvuuia deserti*, *Mononykus olecranus*, and *Microraptor zhaoianus*; although it is unknown in *Archaeopteryx lithographica* and *Confuciusornis sanctus*.

Character 98: Anterior cervical centra (Gauthier, 1986)

0: subcircular or square in anterior view

1: distinctly wider than high, kidney shaped

Character 99: Cervical neural spines (Makovicky and Sues, 1998)

0: anteroposteriorly long

1: short and centered on neural arch, giving arch an X shape in dorsal view

Character 100: Cervical centra (Gauthier, 1986)

0: with one pair of pneumatic openings

1: with two pairs of pneumatic openings

Character 101: Cervical and anterior trunk vertebrae (MODIFIED)

0: amphiplatyan

1: opisthocoelous

2: at least partially heterocoelous

Character 102: Anterior trunk vertebrae (Gauthier, 1986)

0: without prominent hypapophyses

1: with large hypapophyses

Character 103: Parapophyses of posterior trunk vertebrae (Norell and Makovicky, 1999)

0: flush with neural arch

1: distinctly projected on pedicels

Character 104: Hyposphene-hypantrum articulations in trunk vertebrae

0: absent

1: present

Character 105: Zygapophyses of trunk vertebrae

0: abutting one another above neural canal, opposite hyposphenes meet to form lamina

1: lateral to neural canal and separated by groove for interspinous ligaments, hyposphenes separated

Character 106: Cervical vertebrae pneumaticity (MODIFIED to refer to just the cervicals)

0: absent

1: present

Character 107: Transverse processes of anterior dorsal vertebrae

0: long and thin

1: short, wide, and only slightly inclined

Character 108: Neural spines of dorsal vertebrae

0: not expanded distally

1: expanded to form "spine table"

Character 109: Scars for interspinous ligaments

0: terminate at apex of neural spine in dorsal vertebrae

1: terminate below apex of neural spine

Character 110: Number of sacral vertebrae OR DERED

0: 5 or fewer

1: 6

2: 7

3: 8

4: 9

5: 10

6: 11 or more

7: 15 or more

This character has been modified to include the character states of CEA 06 62 to score for the additional derived morphology in derived avialans.

Character 111: Sacral vertebrae

0: with unfused zygapophyses

1: with fused zygapophyses forming a sinuous ridge in dorsal view

Character 112: Ventral surface of posterior sacral centra

0: gently rounded, convex

1: ventrally flattened, sometimes with shallow sulcus

2: centrum strongly constricted transversely, ventral surface keeled

Note that in *Alvarezsaurus calvoi* it is only the fifth sacral that is keeled, unlike other alvarezsaurids (Novas, 1997).

Character 113: Pleurocoels ORDERED

0: absent on sacral vertebrae

1: present on anterior sacrals only

2: present on all sacrals

Character 114: Last sacral centrum

0: with flat posterior articulation surface

1: convex articulation surface

Character 115: Free caudal vertebrae

0: with distinct transition point, from shorter centra with long transverse processes proximally to longer centra with small or no transverse processes distally

1: vertebrae homogeneous in shape, without transition point

Character 116: Transition point in caudal series

0: distal to the 10th caudal vertebra

1: between the 7th and 10th caudal vertebra

2: proximal to the 7th caudal vertebra

New state added by MAE 05. A second state for having the transition point proximal to the 6th vertebra was added specifically to test the purported avialan relationships of *Rahonavis.*

Character 117: Anterior caudal centra (modified from Gauthier, 1986)
0: tall, oval in cross section
1: with boxlike centra in caudals I–V
2: anterior caudal centra laterally compressed with ventral keel

Character 118: Neural spines of caudal vertebrae (Russell and Dong, 1993)
0: simple, undivided
1: separated into anterior and posterior alae throughout much of caudal sequence

Character 119: Neural spines on distal caudals (Russell and Dong, 1993)
0: form a low ridge
1: spine absent
2: midline sulcus in center of neural arch

Character 120: Prezygapophyses of distal caudal vertebrae
0: between 1/3 and 1 centrum length
1: with extremely long extensions of the prezygapophyses (up to 10 vertebral segments long in some taxa)
2: strongly reduced or absent
3: prezygapophyses clasping the posterior surface of neural arch of preceding vertebrae, postzygapophyses negligible

State 3 was added from CEA 06 67 to score the condition present in *Ichthyornis dispar*. Currently state 3 is autapomorphic for that taxon.

Character 121: Number of caudal vertebra (modified from Turner et al., 2007b)
0: more than 40 caudal vertebrae
1: 25–40 caudal vertebrae
2: no more than 25 caudal vertebrae
3: very short, fewer than 8 free caudal vertebrae

This character has been reworded to incorporate CEA 06 64.1, which scores for the tail morphology of derived avialans.

Character 122: Proximal end of chevrons of proximal caudals
0: short anteroposteriorly, shaft cylindrical
1: proximal end elongate anteroposteriorly, flattened and platelike

Character 123: Distal caudal chevrons
0: simple
1: anteriorly bifurcate
2: bifurcate at both ends

Character 124: Shaft of cervical ribs
0: slender and longer than vertebra to which they articulate
1: broad and shorter than vertebra

Character 125: Ossified uncinate processes OR DERED
0: absent
1: present and unfused to ribs
2: fused to ribs

This character was modified to include a third state based on CEA 07 70.2 to score for the morphology present in many extant avians.

Character 126: Ossified ventral (sternal) rib segments
0: absent
1: present

Character 127: Lateral gastral segment
0: shorter than medial one in each arch
1: distal segment longer than proximal segment

Character 128: Ossified sternal plates
0: separate in adults
1: fused

Character 129: Sternum
0: without distinct lateral xiphoid process posterior to costal margin
1: with lateral xiphoid process

Character 130: Anterior edge of sternum
0: grooved for reception of coracoids
1: sternum without grooves

Character 131: Articular facet of coracoid on sternum (conditions may be determined by the articular facet on coracoid in taxa without ossified sternum)
0: anterolateral or more lateral than anterior
1: almost anterior

Character 132: Hypocledium on furcula ORDERED
0: absent
1: present as tubercle
2: present as an elongate process

The hypocledium is a process extending from the ventral midline of the furcula, and is attached to the sternum by a ligament in extant birds. Although a number of taxa such as advanced tyrannosaurids display a slight midline ridge (Makovicky and Currie, 1998), this trait is considered state 0 here. Only a full process as occurs in *Oviraptor,* for example, is considered state 1 in our analysis. MODIFIED. State 1 was divided into two distinct states scoring for the incipient form of a hypocledium as is present in some basal coelurosaurs as well as derived avialans. This modification follows CEA 06 82.start

Character 133: Acromion margin of scapula
0: continuous with blade
1: anterior edge laterally everted

Character 134: Posterolateral surface of coracoid ventral to glenoid fossa
0: unexpanded
1: posterolateral edge of coracoid expanded to form triangular subglenoid fossa bounded laterally by enlarged coracoid tuber

Character 135: Scapula and coracoid
0: separate
1: fused into scapulacoracoid

Character 136: Coracoid in lateral view
0: subcircular, with shallow ventral blade
1: subquadrangular with extensive ventral blade
2: shallow ventral blade with elongate posteroventral process
3: height more than twice width—coracoid strutlike

This character was modified following CEA 06 89. A fourth state was added to score the derived condition in most avialans.

Character 137: Scapula and coracoid
0: form a continuous arc in posterior and anterior views
1: coracoid inflected medially, scapulocoracoid L-shaped in lateral view

Character 138: Glenoid fossa faces
0: posteriorly or posterolaterally
1: laterally

Character 139: Scapula length

0: longer than humerus
1: humerus longer than scapula

Character 140: Deltopectoral crest

0: large and distinct, proximal end of humerus quadrangular or triangular in anterior view
1: deltopectoral crest less pronounced, forming an arc rather than being quadrangular
2: deltopectoral crest very weakly developed, proximal end of humerus with rounded edges
3: deltopectoral crest extremely long and rectangular

(original wording): Deltopectoral crest large and distinct, proximal end of humerus quadrangular in anterior view (0) or deltopectoral crest less pronounced, forming an arc rather than being quadrangular (1) or deltopectoral crest very weakly developed, proximal end of humerus with rounded edges (2) or deltopectoral crest extremely long and rectangular (3) or proximal end of humerus extremely broad, triangular in anterior view (4). In the present context old state 4 was autapomorphic for *Confuciusornis*.

Character 141: Anterior surface of deltopectoral crest

0: smooth
1: with distinct muscle scar near lateral edge along distal end of crest for insertion of biceps muscle

Character 142: Olecranon process

0: weakly developed
1: distinct and large

Character 143: Distal articular surface of ulna (dorsal condyle and dorsal trochlea in birds)

0: flat
1: convex, semilunate surface (1).

MODIFIED. Wording changed slightly following CEA 06.

Character 144: Proximal surface of ulna

0: a single continuous articular facet
1: divided into two distinct fossae (one convex, the other concave) separated by a median ridge

Character 145: Lateral proximal carpal (ulnare?)

0: quadrangular
1: triangular in proximal view

The homology of the carpal elements of coelurosaurs is unclear (see, e.g., Padian and Chiappe, 1998), but the large, triangular lateral element of some taxa most likely corresponds to the lateral proximal carpal of basal tetanurans.

Character 146: Two distal carpals in contact with metacarpals

0: one covering the base of metacarpal I (and perhaps contacting metacarpal II) the other covering the base of metacarpal II
1: a single distal carpal capping metacarpals I and II

In the absence of ontogenetic data, it is not possible to determine whether the single large semilunate carpal of birds and many other coelurosaurs is formed by fusion of the two distal carpals or is, instead, an enlarged distal carpal 1 or 2.

EXCLUDED Character 147: Distal carpals not fused to metacarpals (0) or fused to metacarpals, forming carpometacarpus (1).

This character is excluded in favor of character 390.

Character 148: Semilunate distal carpal

0: well developed, covering all of proximal ends of metacarpals I and II
1: small, covers about half of base of metacarpals I and II
2: covers bases of all metacarpals
3: covers MC II and MC III

In modern birds, the semilunate covers MC II and MC III. This character was modified to include a fourth state for the derived avialan condition in which the semilunate carpal does not cover any portion of metacarpal 1.

Character 149: Metacarpal I

0: half or less than half the length of metacarpal II, and longer proximodistally than wide transversely
1: subequal in length to metacarpal II
2: very short and wider transversely than long proximodistally

Character 150: Third manual digit

0: present, phalanges present
1: reduced to no more than metacarpal splint

Character 151: Manual unguals

0: strongly curved, with large flexor tubercles
1: weakly curved with weak flexor tubercles displaced distally from articular end
2: straight with weak flexor tubercles displaced distally from articular end
3: absent

A fourth state was added to this character in order to score for the absence of unguals in derived avialans.

Character 152: Unguals on all digits

0: generally similar in size
1: digit I bearing large ungual and unguals of other digits distinctly smaller

Character 153: Proximodorsal "lip" on some manual unguals—a transverse ridge immediately dorsal to the articulating surface

0: absent
1: present

Character 154: Ventral edge of anterior ala of ilium

0: straight or gently curved
1: ventral edge with shallow, obtuse process
2: process strongly hooked

Character 155: Preacetabular part of ilium

0: roughly as long as postacetabular part of ilium
1: preacetabular portion of ilium markedly longer (more than 2/3 of total ilium length) than postacetabular part
2: postacetabular blade much longer

MODIFIED. A third character state was added to score the ilium morphology seen in *Hesperornis*.

Character 156: Anterior end of ilium

0: gently rounded or straight
1: anterior end strongly convex, lobate
2: pointed at anterodorsal corner with concave anteroventral edge
3: distinctly concave dorsally

MODIFIED. A fourth character state was added to include the tyrannosaurid morphology as noted by R 03 173.

Character 157: Supraacetabular crest on ilium as a separate process from antitrochanter, forms "hood" over femoral head ORDERED

0: present
1: reduced, not forming hood
2: absent

Character 158: Postacetabular ala of ilium in lateral view

0: squared
1: acuminate

Character 159: Postacetabular blades of ilia in dorsal view
0: subparallel
1: diverge posteriorly

Character 160: Tuber along dorsal edge of ilium, dorsal or slightly posterior to acetabulum
0: absent
1: present

Novas (2004) noted the presence of this tuber on the ilia of *Saurornitholestes langstoni* (MOR 660), *Deinonychus antirrhopus* (AMNH 30115, MCZ 4317), and *Velociraptor mongoliensis* (IGM 100/985), *Unenlagia comahuensis*, *Archaeopteryx lithographica* (Berlin specimen), Enantiornithes (Walker, 1981), *Confuciusornis sanctus* (Chiappe et al., 1999) and *Rahonavis ostromi*. This tuber is considered homologous to the processus supratrochantericus of birds. It is associated with an oblique ridge that runs from the dorsal surface of the acetabulum to the supratrochanteric process. Novas (2004) indicated that, according to Baumel and Witmer (1993), this ridge divides the origin of the m. iliotibialis from the m. iliofemoralis. We cannot find reference to the processus supratrochantericus in Baumel and Witmer (1993). Hutchinson (2001a) reproduces the *Meleagris* pelvic diagram of Baumel and Witmer (1993), illustrating the processus supratrochantericus. However, in both Hutchinson (2001a) and Vanden Berge and Zweers (1993) the processus supratrochantericus and its associated oblique ridge marks the division of the origin of m. iliofemoralis externus from the m. iliofibularis. Given this interpretation, the oblique ridge serves a role similar to that of the "vertical ridge" present in tyrannosauroid ilium—namely the division of the preacetabular concavity from the postacetabular concavity. Here I follow the conclusion of Hutchinson (2001a) and do not consider the "vertical ridge" and the oblique ridge below the supratrochanteric process homologous. Numerous tests of congruence reject this hypothesis as well as an incomplete satisfication of connectivity (e.g., no supratrochanteric process in Tyrannosauroidea).

Character 161: Brevis fossa
0: shelflike
1: deeply concave with lateral overhang

Character 162: Antitrochanter posterior to acetabulum
0: absent or poorly developed
1: prominent

Character 163: Ridge bounding cuppedicus fossa
0: terminates rostral to acetabulum or curves ventrally onto anterior end of pubic peduncle
1: rim extends far posteriorly and is confluent or almost confluent with acetabular rim

Redefined by MAE 05 following description of condition in *Unenlagia* and *Rahonavis* by Novas (2004) as confirmed by personal observation.

Character 164: Cuppedicus fossa
0: deep, ventrally concave
1: fossa shallow or flat, with little or no lateral overhang
2: absent

See (Hutchinson, 2001b) for explanation of related changes in pelvic musculature.

Character 165: Posterior edge of ischium
0: straight
1: with proximal median posterior process

Character 166: Ischium (MAE 05)
0: with rodlike shaft [i.e., part distal to ace tabular portion]
1: with wide, flat, and platelike shaft

Character 167: Ischiadic shaft
0: straight
1: ventrodistally curved anteriorly
2: hooked posteriorly

Character 168: Lateral face of ischiadic blade (MAE 05)
0: flat [or round in rodlike ischia]
1: laterally concave
2: with longitudinal ridge subdividing lateral surface into anterior (including obturator process) and posterior parts

Following MAE 05, some dromaeosaurids have a distinct ridge (i.e., *Sinornithosaurus* and *Buitreraptor*) whereas other the ridge is subtle and forms a slight medial flexure of the obturator process (e.g., *Velociraptor* and *Deinonychus*). These are considered to be homologous.

Character 169: Obturator process of ischium ORDERED
0: absent
1: proximal in position
2: located near middle of ischiadic shaft
3: located at distal end of ischium

Character 170: Obturator process
0: does not contact pubis
1: contacts pubis

Character 171: Obturator notch
0: present
1: notch or foramen absent

Character 172: Semicircular scar on posterior part of the proximal end of the ischium
0: absent
1: present

Character 173: Ischium
0: more than 2/3 of pubis length
1: 2/3 or less of pubis length

Character 174: Distal ends of ischia ORDERED
0: form symphysis
1: approach one another but do not form symphysis
2: widely separated

Character 175: Ischial boot (expanded distal end)
0: present
1: absent

Character 176: Tubercle on anterior edge of ischium
0: absent
1: present

A small tuber occurring along the rostral edge of the ischium between the pubic peduncle and obturator process was described in *Velociraptor* (Norell and Makovicky, 1997) and is also present in *Deinonychus*. (Hutchinson, 2001b) termed this structure the *obturator tuberosity*.

Character 177: Pubis orientation
0: propubic
1: vertical
2: posteriorly oriented (opisthopubic)
3: appressed to ischium

The oviraptorid condition, in which the proximal end of the pubis is vertical and the distal end curves anteriorly, is considered to be state 1. This character was modified to include a fourth state for derived avialans and alvarezsaurids.

Character 178: Pubic boot projects
0: anteriorly and posteriorly
1: with little or no anterior process
2: no anteroposterior projections

Character 179: Shelf on pubic shaft proximal to symphysis ("pubic apron")
0: extends medially from middle of cylindrical pubic shaft
1: shelf extends medially from anterior edge of anteroposteriorly flattened shaft
2: absent
MODIFIED. This character has been modified to include a third state to score the absence of a pubic apron in derived avialans.

Character 180: Pubic shaft
0: straight
1: distal end curves anteriorly, anterior surface of shaft concave
2: shaft curves posteriorly, anteriorly convex curvature
See also (Calvo et al., 2004).

Character 181: Pubic apron
0: about half of pubic shaft length
1: less than 1/3 of shaft length

Character 182: Contact between pubic apron (MAE 05)
0: contributions of both pubes meet extensively
1: contact disrupted by a slit
2: no contact

Character 183: Femoral head
0: without fovea capitalis (for attachment of capital ligament)
1: or circular fovea present in center of medial surface of head

Character 184: Lesser trochanter
0: separated from greater trochanter by deep cleft
1: trochanters separated by small groove
2: completely fused (or absent) to form a trochanteric crest

Character 185: Lesser trochanter of femur
0: alariform
1: cylindrical in cross section

Character 186: Lateral ridge
0: absent or represented only by faint rugosity
1: distinctly raised from shaft, moundlike
Hutchinson (2001a) clarified the terminological confusion surrounding this structure and considered it a derived homolog of the trochanteric shelf of more basal theropods and dinosauromorphs.

Character 187: Fourth trochanter on femur
0: present
1: absent

Character 188: Accessory trochanteric crest distal to lesser trochanter
0: absent
1: present
This character was identified as an autapomorphy of *Microvenator celer* (Makovicky and Sues, 1998), but it is more widespread.

Character 189: Anterior surface of femur proximal to medial distal condyle
0: without longitudinal crest
1: crest present extending proximally from medial condyle on anterior surface of shaft

Character 190: Popliteal fossa between end of femur
0: open distally
1: closed off distally by contact between distal condyles

Character 191: Fibula
0: reaches proximal tarsals
1: short, tapering distally, and not in contact with proximal tarsals

Character 192: Medial surface of proximal end of fibula
0: concave along long axis
1: flat

Character 193: Deep oval fossa on medial surface of fibula near proximal end
0: absent
1: present

Character 194: Distal end of astragalus and calcaneum
0: with condyles separated by shallow, indefinite sulcus
1: with distinct condyles separated by prominent tendoneal groove on anterior surface

Character 195: Tibia, cnemial crest(s)
0: lateral crest only
1: lateral and anterior crests developed (1)
MODIFIED definition following CEA 06 195.

Character 196: Ascending process of the astragalus
0: tall and broad, covering most of anterior surface of distal end of tibia
1: process short and slender, covering only lateral half of anterior surface of tibia
2: ascending process tall, but with medial notch that restricts it to lateral side of anterior face of distal tibia

Character 197: Ascending process of astragalus
0: confluent with condylar portion
1: separated by transverse groove or fossa across base

Character 198: Calcaneum and astragalus ORDERED
0: unfused to each other or tibia in adult
1: fused to each other, unfused to tibia
2: completely fused to each other and tibia
MODIFIED following CEA 06 180.

Character 199: Distal tarsals
0: separate, not fused to metatarsals
1: fuses to metatarsal
MODIFIED. This character was modified to just refer to tarsal/metatarsal fusion.

Character 200: Metatarsals ORDERED
0: not coossified
1: coossification of metatarsals begins proximally
2: metatarsals fuse to each other proximally and distally
3: extreme distal fusion, distal vascular foramen closed
MODIFIED. This character was modified to expand its character states to encompass additional derived states in avialans. (Martin, 1983; Cracraft, 1986; CEA).

Character 201: Distal end of metatarsal II
0: smooth, not ginglymoid
1: with developed ginglymus

Character 202: Distal end of metatarsal III
0: smooth, not ginglymoid

1: with developed ginglymus

Character 203: Metatarsal III proximal shaft

0: prominently exposed between metatarsal II and metatarsal IV along entire metapodium

1: metatarsal III proximal shaft constricted and much narrower than either II or IV, but still exposed along most of metapodium, subarctometatarsal

2: very pinched, not exposed along proximal section of metapodium, arctometatarsal

3: proximal part of metatarsal III lost

Definition following Novas and Pol (2005; their char. 200).

Character 204: Ungual and penultimate phalanx of pedal digit II

0: similar to those of III

1: penultimate phalanx highly modified for extreme hyperextension, ungual more strongly curved and significantly larger than that of digit III

Character 205: Metatarsal I articulates with

0: the middle of the medial surface of metatarsal II

1: the posterior surface of distal quarter of metatarsal II

2: the medial surface of metatarsal II near its proximal end

3: the medial surface of at the distal end

MODIFIED. In the original formulation, State 3 scored for the absence of a metatarsal I. This state was dropped in lieu of a separate character that scores for the presence or absence of metatarsal I (char. 528). A new state was included to score for the location of metatarsal I on the medial side of metatarsal II near the distal end as is seen in many basal avialans (e.g., *Archaeopteryx lithographica* (Mayr et al., 2005), *Jeholornis prima* IVPP V13353, *Yanornis martini* IVPP V12444, *Cathayornis yandica* (Zhou and Hou, 2002), *Concornis lacustris* Sanz et al., 1995), *Liaoningornis longidigitris* (Zhou and Hou, 2002)).

Character 206: Metatarsal I

0: attenuates proximally, without proximal articulating surface

1: proximal end of metatarsal I similar to that of metatarsals II–IV

Character 207: Shaft of metatarsal IV

0: round or thicker dorsoventrally than wide in cross section

1: shaft of metatarsal IV mediolaterally widened and flat in cross section

Character 208: Foot

0: symmetrical

1: asymmetrical with slender metatarsal II and very robust metatarsal IV, excluding flange

Senter et al. (2004) consider the foot of *Sinovenator* to be symmetric contra (Xu et al., 2002a), but examination of the holotype as well as several referred specimens confirms that the proximal part of metatarsal II is mediolaterally compressed while the proximal section of metatarsal IV is broadened, reflecting an incipient stage of asymmetry. Therefore, we follow Xu et al. (2002a) in coding the foot of *Sinovenator* asymmetric (state 1). Although we acknowledge the difficulties in parsing states when characters display a more continuous range of expressions than originally defined, the asymmetric conditions is derived and the homology of even an incipient form of this state needs to be acknowledged and subjected to the test of congruence. If future discoveries reveal more taxa with the incipient condition a separate state may be warranted for it.

Character 209: Neural spines on posterior dorsal vertebrae in lateral view

0: rectangular or square

1: anteroposteriorly expanded distally, fan shaped

Character 210: Shaft diameter of manual phalanx I-1

0: less than shaft diameter of radius.

1: greater than shaft diameter of radius.

Character 211: Angular

0: exposed almost to end of mandible in lateral view, reaches or almost reaches articular

1: excluded from posterior end angular suture turns ventrally and meets ventral border of mandible rostral to glenoid

Character 212: Laterally inclined flange along dorsal edge of surangular for articulation with lateral process of lateral quadrate condyle

0: absent

1: present

Character 213: Distal articular ends of metacarpals I + II

0: ginglymoid

1: rounded, smooth

2: II ginglymoid and metacarpal I shelf

This character has been modified to include the shelf like distal articular surface in derived avialans. This new character state follows CEA 06 146.1.

Character 214: Radius and ulna

0: well separated

1: with distinct adherence or syndesmosis distally

Character 215: Jaws

0: occlude for their full length

1: diverge rostrally due to kink and downward deflection in dentary buccal margin

Character 216: Quadrate head

0: covered by squamosal in lateral view

1: quadrate cotyle of squamosal open laterally exposing quadrate head

Character 217: Brevis fossa

0: poorly developed adjacent to ischial peduncle and without lateral overhang, medial edge of brevis fossa visible in lateral view

1: fossa well developed along full length of postacetabular blade, lateral overhang extends along full length of fossa, medial edge completely covered in lateral view

Character 218: Vertical ridge on lesser trochanter

0: present

1: absent

Character 219: Supratemporal fenestra

0: bounded laterally and posteriorly by the squamosal

1: extends as a fossa on to the dorsal surface of the squamosal

Character 220: Dentary

0: fully toothed

1: only with teeth rostrally

2: edentulous

Character 221: Posterior edge of coracoid

0: not or only shallowly indented below glenoid

1: deeply notched just ventral to glenoid, glenoid lip everted

Character 222: Retroarticular process

0: points caudally
1: curves gently dorsocaudally

Character 223: Flange on supraglenoid buttress on scapula (Nicholls and Russell, 1985)
0: absent
1: present

Character 224: Depression (possibly pneumatic) on ventral surface of postorbital process of laterosphenoid (Makovicky et al., 2003)
0: absent
1: present

Character 225: Basal tubera
0: set far apart, level with or beyond lateral edge of occipital condyle and/or foramen magnum (may connected by a web of bone or separated by a large notch)
1: small, directly below condyle and foramen magnum, and separated by a narrow notch
2: absent

Modified from Makovicky et al., 2003. Basal tubera are absent in IGM 100/1128 and *Mahakala omnogovae* (IGM 100/1033).

Character 226: Dorsal edge of postacetabular blade (Novas, 2004)
0: convex or straight
1: concave, brevis shelf extending caudal to vertical face of ilium giving ilium a dorsally concave outline in lateral view

Character 227: Postacetabular end of ilium (MAE 05 227)
0: terminating in rounded or square end in dorsal view
1: with lobate brevis shelf projecting from end of ilium and beyond end of postacetabular lamina

State 0 occurs in basal dromaeosaurids and basal troodontids whereas *Buitreraptor* and *Microraptor* have a lobate brevis shelf. The reduced brevis shelf of *Unenlagia* also appears to be slightly expanded.

Character 228: Flexor heel on phalanx II-2
0: small and asymmetrically developed only on medial side of vertical ridge subdividing proximal articulation
1: heel long and lobate, with extension of midline ridge extending onto its dorsal surface

MAE 05 228. Advanced troodontids and dromaeosaurids have a well-developed, more symmetric heel, but more basal taxa within each clade including *Sinovenator*, *Microraptor*, *Buitreraptor, Rahonavis* and *Neuquenraptor* display state 0 with a weak, medially skewed heel (see also Senter et al., 2004).

Character 229: Large, longitudinal flange along caudal or lateral face of metatarsal IV
0: absent
1: present

Modified from Novas and Pol (2005). A low, rugose muscle scar is evident along the metaphysis of Metatarsal IV in many theropods and is probably a precursor to the flange considered here. Presence of the rugose scar does not constitute a distinct flange, however, here and is considered to fall under the conditions of state 0 here. Unlike Novas and Pol (2005) we consider the laterally directed flange of *Velociraptor* as homologous with the caudally directed flange in other paravians, because these structure occupy identical topological positions. Likewise, we consider this flange to be present in *Sinornithosaurus*.

Character 230: Proximodorsal process of ischium
0: small, tablike or pointed process along caudal edge of ischium
1: process large proximodorsally hooked and separated from iliac peduncle of the ischium by a notch

MAE 05 203 State 1 occurs in *Unenlagia*, *Rahonavis*, *and Confuciusornis* and in some specimens of *Archaeopteryx* (Berlin, Solnhofen). Other basal paravian taxa that possess a proximodorsal process generally display state 0 including *Buitreraptor*, *Microraptor*, *Sinornithosaurus* and *Sinovenator*.

Character 231: Lateral face of pubic shaft
0: smooth
1: with prominent lateral tubercle about halfway down the shaft

(Senter et al., 2004). State (1) is observed exclusively in the Yixian Fm. dromaeosaurids *Microraptor* and *Sinornithosaurus*.

Character 232: Distally placed dorsal process along caudal edge of ischiadic shaft (Forster et al., 1998)
0: absent
1: present

Character 233: Obturator process
0: square (i.e., with distinct caudal edge or notch)
1: triangular with caudal end confluent with shaft

Character 234: Triangular obturator process with
0: short rostral projection and wide base along ischial shaft
1: short base, long process extending rostrally

State 1 occurs in a number of basal paravians including *Microraptor*, *Sinornithosaurus*, *Sinovenator*, *Rahonavis and Buitreraptor.* Due to incomplete preservations of the ischiadic margin in *Unenlagia*, the condition is difficult to determine, but we view this taxon as having state 1 based on firsthand observation of the holotype.

Character 235: Tuber along extensor surface metatar sal II (associated with the insertion of the tendon of the m. tibialis cranialis in Aves) ORDERED
0: absent
1: present, on approximately the center of the proximodorsal surface of metatarsal II
2: present, developed on lateral surface of metatarsal II, at contact with metatarsal III or on lateral edge of metatarsal III

MODIFIED. This character was modified following CEA 06 198 to include an addition state found in derived avialans.

Character 236: Ulna/femoral length ratio
0: significantly less than one
1: equal or greater than one

Character 237: Dorsal displacement of accessory (maxillary) fenestra
0: absent
1: present

In all non-unenlagiine dromaeosaurids with known cranial material, the maxillary fenestra is displaced dorsally within the antorbital fossa. In other theropods, this displacement is absent with the fenestra positioned more ventrally or central on the medial lamina of the maxilla. Modified from Senter et al., 2004: char. 5.

Character 238: Jugal process of maxilla, ventral to the external antorbital fenestra

0: dorsoventrally narrow

1: dorsoventrally wide

In some dromaeosaurids, such as *Tsaagan mangas* (IGM 100/1015) the jugal process of the maxilla is dorsoventrally wide. In other dromaeosaurids, such as *Velociraptor mongoliensis* (AMNH FR 6515) the jugal process of the maxilla is dorsoventrally narrow. Modified from Senter et al., 2004: char. 14.

Character 239: Accessory antorbital (maxillary) fenestra recessed within a shallow, caudally or caudodorsally open fossa, which is itself located within the maxillary antorbital fossa

0: absent

1: present

All dromaeosaurids with known cranial material exhibit state 1. Witmer (1997: 43) discusses this morphology in detail.

Character 240: Nasal process of maxilla, dorsal ramus (ascending ramus of maxilla):

0: prominent, exposed medially and laterally

1: absent or reduced to slight medial, and no lateral exposure

Most theropods, including *Velociraptor mongoliensis*, have a prominent ascending ramus of the maxilla. In derived avialans this lamina becomes reduced or absent (fig. 8). (modified from Gauthier, 1986, and Cracraft, 1986, by Chiappe, 1996: char. 6, and by Clarke and Norell, 2002: char. 10).

Character 241: In lateral view, participation of the ventral ramus of the nasal process of the maxilla in the anterior margin of the internal antorbital fenestra

0: present extensively

1: small dorsal projection of the maxilla participates in the anterior margin

2: no dorsal projection of maxilla participates in the anterior margin

In most theropods, the ventral ramus of the nasal process of the maxilla forms the anterior margin of the internal antorbital fenestra. A reduction and loss of this ramus is a trend within avialans. Modified from Clarke and Norell, 2002: char. 11.

Character 242: In lateral view, dorsal border of the internal antorbital fenestra formed by

0: lacrimal and maxilla

1: lacrimal and nasal

In all basal avialans, except *Archaeopteryx lithographica*, the nasal forms the dorsal border of the internal antorbital fenestra. In non–avialan theropods, including *Archaeopteryx lithographica*, the dorsal border is formed from the medial lamina of the ascending process of the maxilla.

Character 243: In lateral view, dorsal border of the antorbital fossa formed by

0: lacrimal and maxilla

1: lacrimal and nasal

2: maxilla, premaxilla, and lacrimal

In all basal avialans, including *Archaeopteryx lithographica*, the nasal forms the dorsal border of the antorbital fossa. This is because the ascending process of the maxilla in *Archaeopteryx lithographica* is recessed medially slightly.

Character 244: In lateral view, lateral lamina of the ventral ramus of nasal process of maxilla

0: present, large broad exposure

1: present, reduced to small triangular exposure

The derived state is found in basal dromaeosaurids such as *Sinornithosaurus millenii*, basal troodontids like *Mei long*, and in the new taxon *Shanag ashile.* (Turner et al., 2007a).

Character 245: Supratemporal fossa

0: with limited extension onto dorsal surfaces of frontal and postorbital

1: covers most of frontal process of the postorbital and extends anteriorly onto dorsal surface of frontal

A number of large theropods, dromaeosaurids, and some oviraptorosaurs exhibit state 1. This character is distinguished from character 42, which codes for the shape of the fossa on the frontal and postorbital. Modified from Currie, 1995, by Currie and Varricchio, 2004: char. 14.

Character 246: Jugal

0: does not particulate in margin of antorbital fenestra

1: participates in antorbital fenestra

In *Allosaurus fragilis* and *Oviraptor philoceratops* the jugal does not participate in the margin of the antorbital fenestra.

Character 247: Anterior and posterior denticles of teeth

0: not significantly different in size

1: anterior denticles, when present, significantly smaller than posterior denticles

The anterior and posterior denticles in most theropods as well as *Dromaeosaurus albertensis* exhibit state 0. Most dromaeosaurids exhibit state 1. (see Ostrom, 1969a).

Character 248: Maxillary teeth

0: almost perpendicular to jaw margin

1: inclined strongly posteroventrally

Bambiraptor feinbergorum and *Atrociraptor marshalli* exhibit state 1. Modified from Currie and Varricchio, 2004: char. 40.

Character 249: Maxillary tooth height

0: highly variable with gaps evident for replacement

1: almost isodont with no replacement gaps

State 1 usually depicts no more than a 30% difference in height between adjacent teeth. (Currie and Varricchio, 2004: char. 41).

Character 250: Splenial forms notched anterior margin of internal mandibular fenestra

0: absent

1: present

State 1 is present in *Allosaurus fragilis* and *Tyrannosaurus rex*. (Currie and Varricchio, 2004: char. 35).

Character 251: First premaxillary tooth size compared with crowns of premaxillary teeth 2 and 3

0: slightly smaller or same size

1: much smaller

2: much larger

Modified from Currie, 1995; Currie and Varricchio, 2004: char. 42.

Character 252: Maxilla, promaxillary fenestra in adults

0: visible in lateral view

1: obscured in lateral view by ascending ramus of maxilla

Witmer, 1997. Currie et al., 2003: char. 35.

Character 253: Nasal

0: dorsally flat for most of length

1: dorsally convex
Currie et al., 2003: char. 41.

Character 254: Nasal
0: unfused
1: fused
Holtz, 2001: char. 3. Currie et al., 2003: char. 42.

Character 255: Squamosal-quadratojugal flange constricting infratemporal fenestra
0: absent
1: present
Holtz, 2001: char. 4. Currie et al., 2003: char. 69.

Character 256: Supraoccipital, pronounced, strongly demarcated median ridge
0: absent
1: present
After Holtz, 1998. Currie et al., 2003: char. 70.

Character 257: Surangular, anteroventral extension divides external mandibular fenestra by contacting angular anteriorly
0: absent
1: present
Currie et al., 2003: char. 72.

Character 258: Surangular, posterior surangular foramen
0: small
1: large fenestra
Currie et al., 2003: char. 73. After Holtz, 2001: char. 12.

Character 259: Vertical ridge on iliac blade above acetabulum
0: absent or poorly developed
1: well developed
Molnar et al., 1990. Rauhut, 2003, char. 172.

Character 260: Shape of premaxillary body
0: wider than high or approximately as wide as high
1: significantly higher than wide
Rauhut (2003): char. 1.

Character 261: Dorsal surface of the nasals
0: smooth
1: rugose
Rauhut (2003): char. 18.

Character 262: Sublacrimal part of jugal
0: tapering
1: bluntly squared anteriorly
2: expanded
3: bifurcated
Rauhut (2003): char. 23. In its current form, adapted directly from Rauhut (2003) with one additional state (3), includes a state scoring for the presence of a blunted squared sublacrimal part of the jugal (state 1). Because this analysis is restricted to Coelurosauria no taxon is scored for this trait. Rauhut (2003) scored *Compsognathus longipes* as "0/1" because of ambiguity. Examination of MNHN CNJ 79 clarifies this scoring as state 0. State 1 was retained for future use do to bluntly squared anterior rami of jugals in basal theropods like *Coelophysis* and *Liliensternus liliensterni* (Rauhut, 2003: 53). State 3 (a bifurcated sublacrimal process of the jugal) is present in two basal troodontids from Mongolia.

Character 263: Axial neural spine
0: sheetlike
1: anteroposteriorly reduced and rodlike
Molnar et al. (1990). Rauhut (2003): char. 93.

Character 264: Prezygapophyses in anterior postaxial cervicals
0: straight
1: anteroposteriorly convex, flexed ventrally anteriorly
Modified from Gauthier (1986).

Character 265: Pleurocoels in dorsal vertebrae OR DERED
0: absent
1: present in anterior dorsals
2: present in all dorsals
Holtz (1994) as modified by Harris (1998). Rauhut (2003): char. 106.

Character 266: Ratio femur/humerus ORDERED
0: more than 2.5
1: between 1.2 and 2.2
2: less than 1
Rauhut (2003): char. 139.

Character 267: Humerus in lateral view
0: sigmoidal
1: straight
Holtz (1994). Rauhut (2003): char. 143.

Character 268: Radius
0: more than half the length of humerus
1: less than half the length of humerus
Rauhut (2003): char. 145.

Character 269: (CEA 06 1) Premaxillae ORDERED
0: unfused in adults
1: fused anteriorly in adults, posterior nasal [frontal] processes not fused to each other
2: frontal processes completely fused as well as anterior premaxillae

Character 270: (CEA 06 7) Dentaries
0: joined proximally by ligaments
1: joined by bone

Character 271: (CEA 06 8) Mandibular symphysis, two strong grooves forming an anteriorly opening V in ventral view
0: absent
1: present

Character 272: (CEA 06 9) Facial margin ORDERED
0: primarily formed by the maxilla, with the maxillary process of the premaxilla restricted to the anterior tip
1: maxillary process of the premaxilla extending 1/2 facial margin
2: maxillary process of the premaxilla extending more than 1/2 of facial margin
This character does not overlap with TWiG 20 and character 20. TWiG 20 describes the length that the premaxillary process extends behind the external nares. CEA 06 09 describes how far the maxillary process extends along the facial or ventral margin of the side of the face. This character marks a shift in the morphology of the maxillary process of the premaxilla in early avialans. With the reduction of the maxillary process behind the nares and the elongation of the nares, the maxillary process in derived avialans begins to extend posteriorly along the ventral margin of the face in lateral view.

Character 273: (CEA 06 10) Nasal [frontal] process of premaxilla
0: short
1: long, closely approaching frontal

Character 274: (CEA 06 13) Osseous external naris
0: considerably smaller than the antorbital fenestra
1: larger than the antorbital fenestra

Character 275: (CEA 06 14) Ectopterygoid
0: present
1: absent
Character 276: (CEA 06 15) Articulation between vomer and pterygoid
0: present, well developed
1: reduced, narrow process of pterygoid passes dorsally over palatine to contact vomer
2: absent, pterygoid and vomer do not contact
Character 277: (CEA 06 16) Palatine and pterygoid
0: long, anteroposteriorly overlapping, contact
1: short, primarily dorsoventral, contact
Character 278: (CEA 06 17) Palatine contacts
0: maxillae only
1: premaxillae and maxillae
Character 279: (CEA 06 18) Vomer contacts premaxilla
0: present
1: absent
Character 280: (CEA 06 19) Coronoid ossification
0: present
1: absent
Character 281: (CEA 06 20) Projecting basisphenoid articulation with pterygoid
0: present
1: absent
Character 282: (CEA 06 22) Basisphenoid-pterygoid articulations
0: located basal on basisphenoid
1: located markedly anterior on basisphenoid (parasphenoid rostrum) such that the articulations are subadjacent on the narrow rostrum
Character 283: (CEA 06 23) Basisphenoid-pterygoid articulation, orientation of contact
0: anteroventral
1: mediolateral
2: entirely dorsoventral
Character 284: (CEA 06 24) Pterygoid, articular surface for basisphenoid ORDERED
0: concave "socket," or short groove enclosed by dorsal and ventral flanges
1: flat to convex
2: flat to convex facet, stalked, variably projected
Character 285: (CEA 06 25) Pterygoid, kinked
0: present, surface for basisphenoid articulation at high angle to axis of palatal process of pterygoid
1: absent, articulation in line with axis of pterygoid
Character 286: (CEA 06 26) Osseous interorbital septum (mesethmoid)
0: absent
1: present
Character 287: (CEA 06 27) Osseous interorbital septum (mesethmoid)
0: restricted to posterior or another just surpassing premaxillae/frontal contact in rostral extent does not surpass posterior edge of external nares in rostral extent
1: extending rostral to posterior extent of frontal processes of premaxillae and rostral to posterior edge of external nares
Character 288: (CEA 06 28) Eustachian tubes
0: paired and lateral
1: paired, close to cranial midline
2: paired and adjacent on midline or single anterior opening
Character 289: (CEA 06 29) Eustachian tubes ossified
0: absent
1: present
Character 290: (CEA 06 30) Squamosal, ventral or "zygomatic" process
0: variably elongate, dorsally enclosing otic process of the quadrate and extending anteroventrally along shaft of this bone, dorsal head of quadrate not visible in lateral view
1: short, head of quadrate exposed in lateral view
Character 291: (CEA 06 31) Orbital process of quadrate, pterygoid articulation
0: pterygoid broadly overlapping medial surface of orbital process (i.e., "pterygoid ramus")
1: restricted to anteromedial edge of process
Character 292: (CEA 06 32) Quadrate, orbital process ORDERED
0: pterygoid articulates with anteriormost tip
1: pterygoid articulation does not reach tip
2: pterygoid articulation with no extent up orbital process, restricted to quadrate corpus
Character 293: (CEA 06 33) Quadrate/pterygoid contact
0: as a facet, variably with slight anteromedial projection cradling base
1: condylar, with a well-projected tubercle on the quadrate
Character 294: (CEA 06 34) Quadrate, well-developed tubercle on anterior surface of dorsal process
0: absent
1: present
Character 295: (CEA 06 35) Quadrate, quadratojugal articulation
0: overlapping
1: peg and socket articulation
Character 296: (CEA 06 36) Quadrate, dorsal process, articulation
0: with squamosal only
1: with squamosal and prootic
Character 297: (CEA 06 37) Quadrate, dorsal process, development of intercotylar incisure between prootic and squamosal cotylae
0: absent, articular surfaces not differentiated
1: two distinct articular facets, incisure not developed
2: incisure present, "double headed"
Character 298: (CEA 06 38) Quadrate, mandibular articulation
0: bicondylar articulation with mandible
1: tricondylar articulation, additional posterior condyle or broad surface
Character 299 (CEA 06 39) Quadrate, pneumaticity
0: absent
1: present
Character 300: (CEA 06 40) Quadrate, cluster of pneumatic foramina on posterior surface of the tip of dorsal process
0: absent
1: present
Character 301: (CEA 06 41) Quadrate, pneumatization, large, single pneumatic foramen
0: absent
1: posteromedial surface of corpus
Character 302: (CEA 06 42) Articular pneumaticity
0: absent
1: present

Character 303: (CEA 06 43) Dentary strongly forked posteriorly
0: unforked, or with a weakly developed dorsal ramus
1: strongly forked with the dorsal and ventral rami approximately equal in posterior extent
Character 304: (CEA 06 44) Splenial, anterior extent
0: splenial stops well posterior to mandibular symphysis
1: extending to mandibular symphysis, though noncontacting
2: extending to proximal tip of mandible, contacting on midline
Character 305: (CEA 06 45) Mandibular symphysis, anteroposteriorly extensive, flat to convex, dorsal-facing surface developed
0: absent, concave
1: flat surface developed
Character 306: (CEA 06 46) Mandibular symphysis, symphyseal foramina
0: absent
1: present
Character 307: (CEA 06 47) Mandibular symphysis, symphyseal foramen/foramina
0: single
1: paired
Character 308: (CEA 06 48) Mandibular symphysis, symphyseal foramen/foramina
0: opening on posterior edge of symphysis
1: opening on dorsal surface of symphysis
Character 309: (CEA 06 49) Meckel's groove
0: not completely covered by splenial, deep and conspicuous medially
1: covered by splenial, not exposed medially
Character 310: (CEA 06 50) Anterior external mandibular fenestra
0: absent
1: present
Character 311: (CEA 06 51) Jugal/postorbital contact
0: present
1: absent
Character 312: (CEA 06 52) Frontal/parietal suture
0: open
1: fused
Character 313: (CEA 06 54) Thoracic vertebrae (with ribs articulating with the sternum), one or more with prominent hypapophyses
0: absent
1: present
This character does not address the presence of hypapophyses on transitional vertebrae, or "cervicothoracics," that do not have associated ribs that articulate with the sternum (e.g., Gauthier, 1986; Chiappe, 1996). In contrast, in Aves, well-developed hypapophyses are developed well into the thoracic series, on vertebrae with ribs articulating with the sternum.
Character 314: (CEA 06 55) Thoracic vertebrae, count ORDERED
0: 12 or more
1: 11
2: 10 or fewer
Character 315: (CEA 06 56) Thoracic vertebrae
0: at least part of series with subround, central articular surfaces (e.g., amphicoelous/opisthocoelous) that lack the dorsoventral compression seen in heterocoelous vertebrae
1: series completely heterocoelous
Character 316: (CEA 06 57) Thoracic vertebrae, parapophyses
0: rostral to transverse processes
1: directly ventral to transverse processes (close to midpoint of vertebrae)
Character 317: (CEA 06 58) Thoracic vertebrae, centra, length, and midpoint width
0: approximately equal in length and midpoint width
1: length markedly greater than midpoint width
Character 318: (CEA 06 59) Thoracic vertebrae, lateral surfaces of centra
0: flat to slightly depressed
1: deep, emarginated fossae
2: central ovoid foramina
Character 319: (CEA 06 60) Thoracic vertebrae with ossified connective tissue bridging transverse processes
0: absent
1: present
Character 320: (CEA 06 61) Notarium
0: absent
1: present
Character 321: (CEA 06 63) Sacral vertebrae, series of short vertebrae, with dorsally directed parapophyses just anterior to the acetabulum ORDERED
0: absent
1: present, 3 such vertebrae
2: present, 4 such vertebrae
Character 322: (CEA 06 66) Anterior Free caudals prior to transition point; length of transverse processes
0: subequal to width of centrum
1: significantly shorter than centrum width
Character 323: (CEA 06 68) Distal caudals
0: unfused
1: fused
Character 324: (CEA 06 69) Fused distal caudals, morphology ORDERED
0: fused element length equal or greater than 4 free caudal vertebrae
1: length less than 4 caudal vertebrae
2: less than 2 caudal vertebrae in length
Character 325: (CEA 06 71) Gastralia
0: present
1: absent
Character 326: (CEA 06 71 *revised*) Carina or midline ridge ORDERED
0: absent
1: slightly raised
2: distinctly projected
Character 327: (CEA 06 73) Carina or midline ridge
0: restricted to posterior half of sternum
1: approaches anterior limit of sternum
2: restricted to the anterior half of the sternum
Modified. This character has been modified to include an additional state scoring the morphology present in derived alvarezsaurids.
Character 328: (CEA 06 74) Sternum, dorsal surface, pneumatic foramen (or foramina)
0: absent
1: present

Character 329: (CEA 06 75) Sternum, pneumatic foramina in the depressions (loculi costalis; Baumel and Witmer, 1993) between rib articulations (processi articularis sternocostalis; Baumel and Witmer, 1993)
0: absent
1: present

Character 330: (CEA 06 76) Sternum, coracoidal sulci spacing on anterior edge
0: widely separated mediolaterally
1: adjacent
2: crossed on midline

Character 331: (CEA 06 77) Sternum, number of processes for articulation with the sternal ribs ORDERED
0: 3
1: 4
2: 5
3: 6
4: 7 or more

Character 332: (CEA 06 78) Sternum: raised, paired intermuscular ridges (linea intermuscularis; Baumel and Witmer, 1993) parallel to sternal midline
0: absent
1: present

Character 333: (CEA 06 79) Sternum, posterior margin, distinct posteriorly projected medial and/or lateral processes ORDERED
0: absent (directly laterally projected zyphoid processes developed but not considered homologes as these are copresent with the posterior processes in the new clade)
1: with distinct posterior processes
2: midpoint of posterior sternal margin connected to medial posterior processes to enclose paired fenestra

Character 334: (CEA 06 80) Clavicles
0: fused
1: unfused
Currently state 1 is scored in the dataset only for *Hesperornis*.

Character 335: (CEA 06 81) Interclavicular angle (clavicles elongate)
0: greater than or equal to 90°
1: less than 90°

Character 336: (CEA 06 83) Furcula, laterally excavated
0: absent
1: present
This feature was noted by Chiappe and Calvo (1994) as an enantiornithine synapomorphy.

Character 337: (CEA 06 84) Furcula, dorsal (omal) tip
0: flat or blunt tip
1: with a pronounced posteriorly pointed tip

Character 338: (CEA 06 85) Furcula, ventral margin of apophysis
0: curved, angled
1: with a truncate or squared base

Character 339: (CEA 06 87) Scapula and coracoid articulation
0: pit-shaped scapular cotyla developed on the coracoid, and coracoidal tubercle developed on the scapula ("ball and socket" articulation)
1: scapular articular surface of coracoid convex
2: flat

Character 340: (CEA 06 88) Coracoid, procoracoid process
0: absent
1: present

Character 341: (CEA 06 90) Coracoid, lateral margin
0: straight to slightly concave
1: convex

Character 342: (CEA 06 91) Coracoid, dorsal surface (= posterior surface of basal maniraptoran theropods)
0: strongly concave
1: flat to convex

Character 343: (CEA 06 92) Coracoid, pneumatized
0: absent
1: present

Character 344: (CEA 06 93) Coracoid, pneumatic foramen
0: proximal
1: distal

Character 345: (CEA 06 94) Coracoid, lateral process
0: absent
1: present

Character 346: (CEA 06 95) Coracoid, ventral surface, lateral intermuscular line or ridge
0: absent
1: present

Character 347: (CEA 06 96) Coracoid, glenoid facet
0: dorsal to, or at approximately same level as, acrocoracoid process/"biceps tubercle"
1: ventral to acrocoracoid process

Character 348: (CEA 06 97) Coracoid, acrocoracoid
0: straight
1: hooked medially

Character 349: (CEA 06 98) Coracoid, n. supracor acoideus passes through coracoid
0: present
1: absent

Character 350: (CEA 06 99) Coracoid, medial surface, area of the foramen n. supracoracoideus (when developed)
0: strongly depressed
1: flat to convex

Character 351: (CEA 06 100) Angle between coracoid and scapula at glenoid
0: more than 90°
1: 90° or less

Character 352: (CEA 06 101) Scapula, posterior end
0: wider or approximately the same width as proximal dorsoventral shaft width
1: tapering distally

Character 353: (CEA 06 102) Scapula
0: straight
1: dorsoventrally curved

Character 354: (CEA 06 104) Scapula, acromion process
0: projected anteriorly to surpass the articular surface for coracoid (facies articularis coracoidea; Baumel and Witmer, 1993)
1: projected less anteriorly than the articular surface for coracoid

Character 355: (CEA 06 105) Scapula, acromion process
0: straight
1: laterally hooked tip

Character 356: (CEA 06 106) Humerus and ulna, length ORDERED
0: humerus longer than ulna
1: ulna and humerus approximately the same length
2: ulna significantly longer than humerus

Character 357: (CEA 06 107) Humerus, proximal end, head in anterior or posterior view
0: straplike, articular surface flat, no proximal midline convexity
1: head domed proximally

Character 358: (CEA 06 108) Humerus, proximal end, proximal projection
0: dorsal edge projected farthest
1: midline projected farthest

Character 359: (CEA 06 109) Humerus, ventral tubercle and capital incisure
0: absent
1: present

Character 360: (CEA 06 110) Humerus, capital incisure
0: an open groove
1: closed by tubercle associated with a muscle insertion just distal to humeral head

Character 361: (CEA 06 111) Humerus, anterior surface, well-developed fossa on midline making proximal articular surface appear V-shaped in proximal view
0: absent
1: present

Character 362: (CEA 06 112) Humerus, "transverse groove"
0: absent
1: present, developed as a discreet, depressed scar on the proximal surface of the bicipital crest or as a slight transverse groove

Character 363: (CEA 06 113) Humerus, deltopectoral crest
0: projected dorsally (in line with the long axis of humeral head)
1: projected anteriorly

Character 364: (CEA 06 114) Humerus, deltopectoral crest ORDERED
0: less than shaft width
1: same width
2: dorsoventral width greater than shaft width

Character 365: (CEA 06 115) Humerus, deltopectoral crest, proximoposterior surface
0: flat to convex
1: concave

Character 366: (CEA 06 116) Humerus, deltopectoral crest
0: not perforate
1: with a large fenestra

Character 367: (CEA 06 117) Humerus, bicipital crest, pit-shaped scar/fossa for muscular attachment on anterodistal, distal or posterodistal surface of crest
0: absent
1: present

Character 368: (CEA 06 118) Humerus, bicipital crest, pit-shaped fossa for muscular attachment
0: anterodistal on bicipital crest
1: directly ventrodistal at tip of bicipital crest
2: posterodistal, variably developed as a fossa

Character 369: (CEA 06 119) Humerus, bicipital crest ORDERED
0: little or no anterior projection
1: developed as an anterior projection relative to shaft surface in ventral view
2: hypertrophied, rounded tumescence

Character 370: (CEA 06 120) Humerus, proximal end, one or more pneumatic foramina
0: absent
1: present

Character 371: (CEA 06 121) Humerus, distal condyles
0: developed distally
1: developed on anterior surface of humerus

Character 372: (CEA 06 122) Humerus, long axis of dorsal condyle
0: at low angle to humeral axis, proximodistally orientated
1: at high angle to humeral axis, almost transversely orientated

Character 373: (CEA 06 123) Humerus, distal condyles
0: subround, bulbous
1: weakly defined, "straplike"

Character 374: (CEA 06 124) Humerus, distal margin
0: approximately perpendicular to long axis of humeral shaft
1: ventrodistal margin projected significantly distal to dorsodistal margin, distal margin angling strongly ventrally (sometimes described as a well-projected flexor process)

Character 375: (CEA 06 125) Humerus, distal end, compressed anteroposteriorly and flared dorsoventrally
0: absent
1: present

Character 376: (CEA 06 126) Humerus, brachial fossa
0: absent
1: present, developed as a flat scar or as a scar-impressed fossa

Character 377: (CEA 06 127) Humerus, ventral condyle
0: length of long axis of condyle less than the same measure of the dorsal condyle
1: same or greater than same measure of the dorsal condyle

Character 378: (CEA 06 128) Humerus, demarcation of muscle origins (e.g., m. extensor metacarpi radialis in Aves) on the dorsal edge of the distal humerus
0: no indication of origin as a scar, a pit, or a tubercle
1: indication as a pit-shaped scar or as a variably projected scar-bearing tubercle or facet

Character 379: (CEA 06 129) Humerus, distal end, posterior surface, groove for passage of m. scapulotriceps
0: absent
1: present

Character 380: (CEA 06 130) Humerus, m. humero tricipitalis groove
0: absent
1: present as a ventral depression contiguous with the olecranon fossa

Character 381: (CEA 06 131) Ulna, cotylae
0: dorsoventrally adjacent
1: widely separated by a deep groove

Character 382: (CEA 06 132) Ulna, dorsal cotyla convex
0: absent
1: present

Character 383: (CEA 06 134) Ulna, distal end, dorsal condyle, dorsal trochlear surface, extent along posterior margin
0: less than transverse measure of dorsal trochlear surface
1: approximately equal in extent
Character 384: (CEA 06 135) Ulna, bicipital scar ORDERED
0: absent
1: developed as a slightly raised scar
2: developed as a conspicuous tubercle
Character 385: (CEA 06 136) Ulna, brachial scar
0: absent
1: present
Character 386: (CEA 06 137) Radius, ventroposterior surface
0: smooth
1: with muscle impression along most of surface
2: deep longitudinal groove
Character 387: (CEA 06 138) Ulnare
0: absent
1: present
Character 388: (CEA 06 139) Ulnare
0: "heart shaped," little differentiation into short dorsal and ventral rami
1: V-shaped, well-developed dorsal and ventral rami
Character 389: (CEA 06 140) Ulnare, ventral ramus (crus longus, Baumel and Witmer, 1993)
0: shorter than dorsal ramus (crus brevis)
1: same length as dorsal ramus
2: longer than dorsal ramus
Character 390: (CEA 06 141) Semilunate carpal and metacarpals ORDERED
0: no fusion
1: incomplete proximal fusion
2: complete proximal fusion
3: complete proximal and distal fusion
Character 391: (CEA 06 143) Metacarpal III, antero posterior diameter as a percent of same dimension of metacarpal II
0: approximately equal or greater than 50%
1: less than 50%
Character 392: (CEA 06 144) Metacarpal I, ante roproximally projected muscular process ORDERED
0: absent no distinct process visible
1: small knob at anteroproximal tip of metacarpal
2: tip of process just surpasses the distal articular facet for phalanx 1 in anterior extent
3: tip of extensor process conspicuously surpasses articular facet by approximately half the width of facet, producing a pronounced knob
4: tip of extensor process conspicuously surpasses articular facet by approximately the width of facet, producing a pronounced knob
Character 393: (CEA 06 145) Metacarpal I, anterior surface
0: roughly hourglass shaped proximally, at least moderately expanded anteroposteriorly, and constricted just before flare of articulation for phalanx 1
1: anterior surface broadly convex
Character 394: (CEA 06 147) Pisiform process
0: absent
1: present
Character 395: (CEA 06 148) Carpometacarpus, ventral surface, supratrochlear fossa deeply excavating proximal surface of pisiform process
0: absent
1: present
Character 396: (CEA 06 149) Intermetacarpal space (between metacarpals II and III)
0: reaches proximally as far as the distal end of metacarpal I
1: terminates distal to end of metacarpal I
Character 397: (CEA 06 150) Carpometacarpus, distal end, metacarpals II and III, articular surfaces for digits
0: metacarpal II subequal or surpasses metacarpal III in distal extent
1: metacarpal III extends further
Character 398: (CEA 06 151) Intermetacarpal process or tubercle ORDERED
0: absent
1: present as scar
2: present as tubercle or flange
Character 399: (CEA 06 152) Manual digit II, phalanx 1
0: subcylindrical to subtriangular
1: strongly dorsoventrally compressed, flat caudal surface
Character 400: (CEA 06 153) Manual digit II, phalanges
0: length of phalanx II-1 less than or equal to that of II-2
1: longer
Character 401: (CEA 06 154; Clarke and Chiappe, 2001) Manual digit II, phalanx 2, internal index process on posterodistal edge
0: absent
1: present
Character 402: (CEA 06 155) Ilium, ischium, pubis, proximal contact in adult ORDERED
0: unfused
1: partial fusion (pubis not ankylosed)
2: completely fused
Character 403: (CEA 06 156) Ilium/ischium, distal coossification to completely enclose the ilioischiadic fenestra
0: absent
1: present
Character 404: (CEA 06 158; CN 02 156) Ischium, dorsal process
0: does not contact ilium
1: contacts ilium
Character 405: (CEA 06 160; CN 02 158) Laterally projected process on ischiadic peduncle (antitrochanter)
0: directly posterior to acetabulum
1: posterodorsal to acetabulum
Character 406: (CEA 06 161; CN 02 159) Ilium, preacetabular pectineal process (Baumel and Wit mer, 1993) ORDERED
0: absent
1: present as a small flange
2: present as a well-projected flange
Character 407: (CEA 06 162; CN 06 160) Preacetabular ilium
0: approach on midline, open, or cartilaginous connection

1: coossified, dorsal closure of "iliosynsacral canals"

Character 408: (CEA 06 163; CN 02 161) Preacetabular ilium extends anterior to first sacral vertebrae
0: no free ribs overlapped
1: one or more ribs overlapped

Character 409: (CEA 06 164; CN 02 162) Postacetabular ilium
0: dorsoventrally orientated
1: mediolaterally orientated

Character 410: (CEA 06 165; CN 02 163) Postacetabular ilium, ventral surface, renal fossa developed
0: absent
1: present

Character 411: (CEA 06 166; CN 02 164) Ilium, m. cuppedicus fossa as broad, mediolaterally oriented surface directly anteroventral to acetabulum
0: present
1: surface absent, insertion variably marked by a small entirely lateral fossa anterior to acetabulum

Character 412: (CEA 06 169; CN 02 166) Pubis
0: suboval in cross section
1: compressed mediolaterally

Character 413: (CEA 06 170; CN 02 167) Pubes, distal contact
0: contacting, variably coossified into symphysis
1: noncontacting

Character 414: (CEA 06 173; Chiappe, 1991) Femur, posterior trochanter ORDERED
0: present, developed as a slightly projected tubercle or flange
1: hypertrophied, "shelflike" conformation (in combination with development of the trochanteric shelf; see Hutchinson, 2001a)
2: absent

Character 415: (CEA 06 175) Femur, patellar groove
0: absent
1: present

Character 416: (CEA 06 176) Femur, ectocondylar tubercle and lateral condyle
0: separated by deep notch
1: form single trochlear surface

Character 417: (CEA 06 177) Femur, posterior projection of the lateral border of the distal end, continuous with lateral condyle
0: absent
1: present
This corresponds to the caudal intermuscular line that slants down to the medial

Character 418: (CEA 06 178) Laterally projected fibular trochlea ORDERED
0: absent
1: present, developed as small notch
2: a shelflike projection

Character 419: (CEA 06 182) Tibia/tarsal formed condyles
0: medial condyle projecting further anteriorly than lateral
1: equal in anterior projection

Character 420: (CEA 06 183) Tibia/tarsal formed condyles, extensor canal ORDERED
0: absent
1: an emarginated groove
2: groove bridged by an ossified supratendoneal bridge

Character 421: (CEA 06 184) Tibia/tarsal formed condyles, tuberositas retinaculi extensoris (Baumel and Witmer, 1993) indicated by short medial ridge or tubercle proximal to the condyles close to the midline and a more proximal second ridge on the medial edge
0: absent
1: present

Character 422: (CEA 06 185) Tibia/tarsal formed condyles, mediolateral widths ORDERED
0: medial condyle wider
1: approximately equal
2: lateral condyle wider

Character 423: (CEA 06 186) Tibia/tarsal formed condyles
0: gradual sloping medial constriction of condyles
1: no medial tapering of either condyle

Character 424: (CEA 06 187) Tibia/tarsal formed condyles, intercondylar groove
0: mediolaterally broad, approximately 1/3 width of anterior surface
1: less than 1/3 width of total anterior surface

Character 425: (CEA 06 188) Tibia, extension of articular surface for distal tarsals/tarsometatarsus ORDERED
0: no posterior extension of trochlear surface, or restricted to distalmost edge of posterior surface
1: well-developed posterior extension, sulcus cartilaginis tibialis of Aves (Baumel and Witmer, 1993), distinct surface extending up the posterior surface of the tibiotarsus
2: with well-developed, posteriorly projecting medial and lateral crests

Character 426: (CEA 06 189) Tibia, distalmost mediolateral width
0: wider than midpoint of shaft, giving distal profile a weakly developed triangular form
1: approximately equal to shaft width, no distal expansion of whole shaft, although condyles may be variably splayed mediolaterally

Character 427: (CEA 06 192) Metatarsal V
0: present
1: absent

Character 428: (CEA 06 193) Metatarsal III
0: proximally in plane with II and IV
1: proximally displaced plantarly, relative to metatarsals II and IV

Character 429: (CEA 06 194) Tarsometatarsus, inter cotylar eminence
0: absent
1: well developed, globose

Character 430: (CEA 06 195) Tarsometatarsus, projected surface or grooves on proximoposterior surface (associated with the passage of tendons of the pes flexors in Aves; hypotarsus) ORDERED
0: absent
1: developed as posterior projection with flat posterior surface
2: projection, with distinct crests and grooves
3: at least one groove enclosed by bone posteriorly

Character 431: (CEA 06 196) Tarsometatarsus, proximal vascular foramen (foramina) ORDERED
0: absent
1: one, between metatarsals III and IV
2: two

Character 432: (CEA 06 197) Metatarsal I ORDERED
0: straight
1: curved or distally deflected but not twisted, ventral surface convex "J shaped"
2: deflected and twisted such that the ventromedial surface is concave proximal to trochlear surface for phalanx I

Character 433: (CEA 06 199) Metatarsal II, distal plantar surface, fossa for metatarsal I ORDERED [fossa metatarsi I; Baumel and Witmer, 1993]
0: absent
1: shallow notch
2: conspicuous ovoid fossa

Character 434: Metatarsals, relative mediolateral width
0: metatarsal IV approximately the same width as metatarsals II
1: metatarsal IV narrower than MII and MIII
2: metatarsal IV greater in width than either metatarsal II or III
MODIFIED from CEA 06 201

Character 435: Metatarsals, comparative trochlear width
0: II approximately the same size as III and/or IV
1: II wider than III and/or IV
2: II narrower than III and/or IV
3: IV narrowest.
MODIFIED. A fourth character state has been added to CEA 06 202

Character 436: (CEA 06 203) Distal vascular foramen
0: simple, with one exit
1: forked, two exits (plantar and distal) between metatarsals III and IV.

Character 437: (CEA 06 204) Metatarsal III, trochlea in plantar view, proximal extent of lateral and medial edges of trochlea
0: absent, trochlear edges approximately equal in proximal extent
1: present, lateral edge extends further

Character 438: (CEA 06 205) Metatarsal II, distal extent of metatarsal II relative to metatarsal IV ORDERED
0: approximately equal in distal extent
1: metatarsal II shorter than metatarsal IV, but reaching distally further than base of metatarsal IV trochlea
2: metatarsal II shorter than metatarsal IV, reaching distally only as far as base of metatarsal IV trochlea.

Character 439: [NEW] Middle to posterior caudal vertebrae
0: 2x or less the length of dorsal vertebrae
1: 3x–4x length of dorsal vertebrae

Character 440: [NEW] Coracoid fenestra
0: absent
1: present

Character 441: [NEW] Metatarsal V, elongated and bowed
0: absent
1: present

Character 442: [NEW] Posterior extension of caudal chevrons
0: not significantly elongated
1: very elongated

Character 443: [NEW] Radius width
0: roughly half or greater than width of ulna
1: less than half width of ulna

Character 444: [NEW] Combined length of metacarpal I plus phalanx I-1
0: greater than length of metacarpal II
1: equal to or less than length of metacarpal II

Character 445: [NEW] Metacarpal III
0: straight
1: bowed

Character 446: [NEW] Metatarsal I
0: distal end of trochlea proximally placed relative to other metatarsals
1: inline distally with others
This is an Enantiornithes synapomorphy.

Character 447: [NEW] Metatarsal I
0: present
1: absent

Character 448: [NEW] Development of the preotic pendent ORDERED
0: absent
1: present but small
2: present and robust

Character 449: [NEW] Shape of the metotic strut
0: short and robust
1: long and narrow

Character 450: [NEW] Prootic recess ORDERED
0: absent
1: present and shallow
2: present and deep

Character 451: [NEW] Anterior tympanic recess (ATR)
0: absent (i.e., not deeply impressed into the lateral wall of basisphenoid)
1: present and impressed into the lateral wall of the basisphenoid
Presence of the ATR creates a distinct crest or angle marking the posterior and dorsal border of the ATR. This crest I will refer to as the *anterior tympanic crista.*

Character 452: [NEW] Location of ATR and the anterior tympanic crista
0: below cranial nerve VII exit just proximal to the otic recess
1: anteriorly with little or no development posterior to the basipterygoid processes

Character 453: [NEW] ATR confluent with the subotic recess
0: absent
1: present, forming the lateral depression

Character 454: [NEW] V-shaped opening between basal tubera remnants
0: absent
1: present
This is probably a remnant of the craniopharyngeal foramen/duct.

Character 455: [NEW] Small tubera (not basal tubera) medial to basal tubera (or basal tubera remnants) and ventral to occipital condyle
0: absent
1: present

Character 456: [NEW] Pedal phalanx II-2, distal articular surface relative to proximal articular surface
0: approximately equal in size, distal surface slightly smaller than proximal
1: distal surface less than half the size of proximal surface

Character 457: [NEW] Sternal plates
0: unossified
1: ossified

Character 458: [NEW] Ulna, size of proximal cotylae
0: unequal, lateral (dorsal in birds) smaller
1: equal

Character 459: [NEW] Middle ear resides within the lateral depression
0: absent
1: present

Character 460: [NEW] Filamentous integumentary structures (stage 1 feathers)
0: absent
1: present

Character 461: [NEW] Vaned feathers (stage 4 feathers)
0: absent
1: present

Character 462: [NEW] Quadratojugal size
0: large
1: greatly reduced

Character 463: [NEW, based on Currie, 1985] Notch for postorbital contact on postorbital process of frontal
0: absent, process smooth or facet small
1: large notch present

Character 464: [NEW] Position of frontoparietal suture relative to postorbital processes of frontal
0: well posterior to the postorbital processes
1: at the level of the postorbital processes
2: anterior to postorbital processes

Character 465: [NEW] Orientation of articular surfaces between cervical vertebrae
0: surfaces vertical to subvertical
1: strongly slanted anteroventrally

Character 466: [NEW] Accessory depression in supra temporal fossa
0: absent
1: present

Character 467: [NEW] Relative ventral extension of pubic versus ischiadic peduncles
0: equal
1: pubic peduncle extends farther ventrally

Character 468: [NEW, partially reworded from char. 6] Ala parasphenoidalis
0: absent
1: present, well developed and crest shaped, forming anterior edge of enlarged pneumatic recess with the ala continuous with the anterior tympanic crista

Character 469: (Nesbitt et al., 2009) Cross section of the furcula
0: nearly circular
1: anteroposteriorly compressed near the symphysis

The furculae from more basal members of the Theropoda (e.g., *Coelophysis*) are rounded in cross section. Oviraptorid furculae are more oval in cross section but still differ from the anteroposteriorly compressed furculae in most paravians whereas the furcula of *Suchomimus* is D-shaped in cross section (Lipkin, 2007).

Character 470: (Nesbitt et al., 2009) General shape of the furcula
0: V-shaped
1: U-shaped

The unfused articulated clavicles in *Massospondylus* are V-shaped. This shape is found in most of the early theropods with furculae including "*Syntarsus*" *kayentakatakae*, *Suchomimus,* and *Allosaurus*. The furculae of all coelurosaurs except *Velociraptor* and those of *Coelophysis rhodesiensis* and *Coelophysis bauri* are U-shaped.

Character 471: (Nesbitt et al., 2009) Epicledial processes
0: unexpanded
1: expanded

The furculae of most theropods have unexpanded epicledial processes. Expanded epicledial processes are present in tyrannosaurids as identified by Makovicky and Currie (1998). Some variation in the size of the epicledial processes is present in *Allosaurus* as noted by Chure and Madsen (1996). The slight expansion of the epicledial processes in *Allosaurus* is smaller than the expansion of the epicledial processes of tyrannosaurids.

Character 472: (Nesbitt et al., 2009) Lateral expansion of the rami between the hypocledium and the epicledial process
0: absent
1: present

The ramus of the furcula normally is the same width as the epicledial processes and the hypocledium region. Oviraptorids have an expanded ramus.

Character 473: (Nesbitt et al., 2009) Hypocledium
0: rounded
1: keeled

The hypocledium of oviraptorids is either smooth or keeled. A keeled hypocledium is present in *Oviraptor* and "big momma" (IGM 100/979).

Character 474: (Nesbitt et al., 2009) Furcula
0: asymmetrical
1: nearly symmetrical

The furculae of most nonparavian theropods are highly asymmetrical (e.g., *Allosaurus, Citipati*). The furculae of paravians, with the exception of *Buitreraptor,* are nearly symmetrical. It is not clear if the asymmetry of the furcula of *Buitreraptor* was the result of taphonomy or represents real morphology.

Character 475: (Nesbitt et al., 2009) Furcula rami
0: thin
1: thick

This refers to the thickness of the rami and hypocledium region. With the exception of *Mei, Archaeopteryx*, *Confuciusornis*, and *Changchengornis* all nonavian theropods have relatively thin furculae. The furculae of *Mei*, *Archaeopteryx*, *Confuciusornis*, and *Changchengornis* all have thick, robust furculae.

Character 476: Anterior (dorsal) surface of metatarsal III
0: relatively narrow and flat
1: transversely expanded and slightly concave

Modified from character 69 of Longrich and Currie (2009).

Character 477: (Turner et al., 2009) Accessory longitudinal ridge on anterolateral side of the distal end of metatarsal IV
0: absent
1: present

APPENDIX 3

Data Matrix

A nexus file of the complete dataset is available on Morphobank (O'Leary and Kaufman, 2007; http://www.morphobank.org or http://morphobank.org/permalink/?660).

Allosaurus fragilis

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Velociraptor mongoliensis
?0110010010000120112000010111000111000121111?10?0100010000111010
0000001001111100010100101000011000110011111101111100011011112111
0010111111111001001110000001002211101110102201011112112011111?00
0000000111011010010000000001100000000011?0010101010000011100110
0000000000011100000000000?0000000?0000??0000000?0000??0000?00
000000(01)0?00??000?000000200 0?000?0000011000?0?001000???000000
00000010100???00000??0100000?0000000000000000000000000000?01
00000000010(12)1100001101100011100000?1000

Balaur bondoc
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??1?1??1???0???10???????
?0????111{01}11101001?11?00001???0???0111?102?01?0?1?2122?????
??????????2110001001000??00??1??????????0?00??0?????????????
????????1?????2?00???
00000200?(01)???0?????????????20??????0???0011000?0?001000???000
?00?????010?00???21??0?00000020?100??0000??????00???0?000000000
?00??0?00000????????010????????1????????00

Atrociraptor marshalli
??????????????????(02)00?0??1010?????????????????????????????
????00??010?????????0?0000101001?????????????????????????????
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??????????????????????????0????0??????????????????11?00??0??111
??????????1??????????0????????????????????????????0????0???
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Utahraptor ostrommaysorum
??????????????????(02)00?0??????????0?001?????????????????????
????????????????????0????0101??1????0?1100?1??1????????0??011???
??????????101?1?????????????0?????????0?01?????????????10????011
1?00??0?0010001001??10?????????11??0???????0?????0?????????1??
?0?????????0???10???0???0?????????????????????????????????????
??00000?????????????????????20000?000000?????????????????????
????????????????????????????00???????0??000000000000?0000?????0?
00?????????????????????????????????????

Adasaurus mongoliensis
?0110?????0????2?????????????????0?????0?1??11?1?0?10001??001??0??
???0????0?1???0?????????????01100?11?0111?10?111(01)100??011?1?
1??????1?111111?????????????????10221110101012201?1?11211001?111
000000?000?11010010010??00??00110?0?0?0001??00100??1??????11???
????00?00?0???1?????????0?????????00??00???000?0??????????00
0?0010000(01)0?????????????????200?0???00??00110?????????????????
????????????????????????????00?000000000000000000000000000?002
??10?00???00???110000??0??0001?1?????????0

Achillobator giganticus
?????????????????????????01?1?????????????????????????????????
??????????????????0000101?????0?01100?11110???????0??011?11???
???????101?????????????00??10220??1101000210 1?011010?001?21110?
0????00?000?101????0???????1???0????001??00100011100??0??100???
??????0???0
000?????????????????????20000?0?0?0?0??10?????????????????????
????????????????????00???0?00000??000???????0?0000????????0?
?????????????0?????????0?????????

Tsaagan mangas
?0110010010000120112000010101000 1?10001211111000100011000010 0??
0000001 00?1111000101001010000110 0??1?????0?????????????????1??
??????11?111???
??????????????????????00??00??00?0000?????????1110000011?00?00
000000?00001???0000000???0000000?0000??000000000000???000???

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??????????????????????????20000???0?0?0??10?????????????????????
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??????0111000???0??00011?0?????????
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Saurornitholestes langstoni

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?????????????????????????????????????????111?????????????11???
?0?????????????????100101?00?11000110011111011011100?1011?1?1??
??????????111?????????000111221?1?1?1?1?0?????????????????11??
0????00??001101??00???00?0?1??00?0000010?001000???????11100011?
??????0????1210???????0?????????????????????00000?????????0???
?????????????????????????0???00??1?????????????????????????
?????????????????????0?????????????????????????????????????0?
??00?????????0?????00111???????00
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Bambiraptor feinbergorum

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?0110??001000012010(02)00?010111000?110001211?10001?0?1?00011?
0?0?000?0100?1111000?0100101002?1110?1100?1??100?0?1100(01)1011
??2????0101011011110?001?1?00000111?211?0101?1022017111021100??
?111000000000100011101?0000000000011000000000011?0010?0101002?11?
110??0000?00000001210002?0000?0??000000??0000??000000001?000??0
0000000010002?0?0?0?0?0?00000200000000002?001?000?0?0?1000??0000
00000?00010?????00000??0000000?000?0000000000000000000000000?00
?010?10000000011100001102?000111011002?1000
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Tianyuraptor ostromi

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??11?????????????????0????111?????????????0??1?????????????????
?????????????????0?0?0?1010??0???0?????????0?0?0?1??01?0111?????
??1??00?011110?001?10100001112?1??0?1101223?11111021?0???1?110?
?????????00?11????000??0???1??00?0??1???1011?0???0??????1?0????
???????0????1?000?0?????????????????????????????????????????0????
??????0?00?00????00000?0?00?000?0?0?????????????????????????????
?????????????????????00?1?0????10?????????????0?0?????????10?1
01???????????1?????????????0000?10??
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Sinornithosaurus millenii

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0011??????0?????????00???1110????10001111002?1???0?01??0???????
?00?00100??1????0100100??100?????????1??1?????0???00?1??1??????
?01?1?11011110?0????0?0000?00?201?01?111023?1?111021?2?1???1???
??????110001?1100?0?00010001??0000???0110111100100000111100?00
?00?????00???10000?000??????0??000????0????00000??1000??00?00?0
?????0?0??0???????00?0?(12)0000???0?000000?00?0??010?0??00?????
?????????????????0000??0000?0000??0?0?00????000??0?0000?00?0???0
011?11000????????01??10000111?1100?1000
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Microraptor zhaoianus

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0?????????????????100?????????????????????????????????????????
??0??010?0?1????0?01000000????001?1??01?1100?01??0110?1212111
?01?101111111010??11010000110121117?0111023?1?1110211201?11111?
?00?000111011111?100??000?11?000????10101111000?0?0???1?110???0
?00???0?00???10??0?000?????????????????????????????0?0???????000
01000?(01)0?00?0000?0010002000???0?000?00???10?0???10100?000??1?
0?000?????????000??????0?00?000000000???000?00??000000000??1
111111??00?0110??011011???1?1?1100?1000
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Graciliraptor lujiatunensis

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????????????????????????????????????????????????????????????????
??????????????????020???1?????????????????????????0???11?12???
???????????????01011?10100001?????????????????????????????????
?0??0?010?(01)11?1??0??0??00?????????????0?????????????????00
????????????????100?????????????????????????????????????????
??????????????????????????????????????????0??????10?0???000??0
??????????10?0000??00?000?????????????????????????????????????
?????10?????????????????????????????
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Hesperonychus elizabethae

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????????????1?????????????1?????????0??1?????????????????????
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Pyroraptor olympius
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??0????????1????????
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??????????01??1????????0?????????????0??????0?????????????????
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??010??0??
?0??????????????????????????????????

Rahonavis ostromi
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????????????????????0????????????0111111???1?01?011112?12???
????????0??11??011???????0?01111?10111110?3?1012101?121??211100
01000?011101101?0100????0??1?????0??10001011111?????????????????
??0
011000(01)0?????????????????2???????????0100?????????????????????
?????010100?????????????????000000?00000000010000000?00000000?00
0??01???0????????0?1?11?????1????????00

Buitreraptor gonzalezorum
?0110?????????????????00001011?00??????????100?10??0011?0????????
?00??001?????????????0210??100?001011110011?110???100011012(012)1
21??????????1101111010?1?10??0??????11?101??11(02)23??01?1?1?120?
??11?0??0??1?011?0?1110000?????0??1????????1101000110000000???0
??????0000??00?00?10100?00?0??????????0????????0?000101???0???
??000000000000(01)0??????????01000100?0?0?00??0?10000?0?001100??
000001000000001?100?????????????????000????00???0?00??????????0?00
?000?0000?00?????????????????1????0010??1100?0000

'Neuquenraptor + Unenlagia'
??
??1111111111??1????1????
????????0??1001???????????????01111?10111110220101111?111202011?100
00??0?010??111100000????0??11????0??110110?110?????????????????
??????0?????210???0?0
0000?0?????????????????1???????????0100?0?0?0011000?00000?????
???????0?????????????????00000?000000000000000000?00000000?00???
????????????????????????????????????

Austroraptor cabazai
?0100?????????????????????1?0????????12?0001?????????????????
???0?011??????????????210??10????0011?001????11?????????????????
????????????00?????????0?????????????????????????????????????1??
????0?0?0?0??{12}1??????????0????0?????????????????00?00??01??00
?????????????1{12}10??0?0?????????????????????????????????????
??0??00?00?????????????????????????????????????0?0?001100???00?
?0000000???
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Unenlagia (combined scoring)
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??1111111111??1????1????
????????0??1001???????????????01111?10111110220101111?111202011?100
0?????????????1????0???????11????0??110?10?11?????????????????
???????????210???0?0
0000?0?????????????????1???????????0100?0?0?0011000?00000?????
????????????????????????00000?000000000000??????00?????????????
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Unenlagia comahuensis

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????????????????????????????????????????????????????????????????????
????????????????????????????????????????1111111111???1????1????
????????0??1001?????????????01111?10111110220101117111202011?100
0?????????????????????0???????11????0??11??10?11?????????????????
???????????????10?????????????????????????????????????????????????0?0
0000?0?????????????????1???????????0100?0?0?0011000?00????????
?????????????????????????00000?000000000000?????00?????????????????
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Unenlagia paynemili

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????????????????????????????????????????????????????????????????????
????????????????????????????????????1?1?????????????????
???????????????0?????????????????1?101????????????11120????????
?????????????????1???????????????1????????110??0?????????????????????
???????????????(12)?????????????????????????????????????????????????
????????????????????????????????????????????0?0?0?11?????000??
????????????????????????????????????0??00?????????????????????????
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Neuquenraptor argentinus

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????????????????????????????????????????????????????????????????????
????????????????????????????????????????????????????????????????????
????????????????????????????????????????????????????????????????????1??
????0?010?0111100000?????????????????????01?????0?????????????????
????????????????????????????????????????????????????????????????????
????????????????????????????????????????????????????????????????????
???????0?????????????????????????????????00000000?00000000?00???
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Shanag ashile

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?????????????????????1??1010110?????????????????????????????????????
?00??011?????????0100101l?????????????????????????????????????????
????????????????????????????????????????????????????????????????????
????????????????????????0????0?????????????????10100001??00???
??????????????????00??0?????????????????????????????????????????????
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Mahakala omnogovae

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?????????????????101?????????????????????????1?00?????????0?0011????
????????????????????02????1???00??0?11?011?111??1?10001101211O???
??????????????00??11100000?100?211101?2?????????????????????0111100
????0?011001101?00000??00??11?0?????0000?????00?????????0???????
??????0????1(01)1?0??????0?????????????????????0??1?000??????????0
000010000(01)0?????????????????????????????00??(01)0???0?0000???
0?????????????100????0??0???000000??0??001??0???000000000?00000
000?000??00?000????1???0??????011?0????????00
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Mononykus olecranus

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??????00???????112????????????????????????????????????????100?????
????????????????????2????0????????1?1?11101101?????10?2???????1??
?1000?00020003011O?112201100??1????1??000?0?1?????3??0???210100
111011211100030000001??00???1??0?0??00?0?0???00?????????????????
???????????10011?????????????????????????????1?????????????????0?0
010???????220???00?????2???0?0?0?0?001?0110??0002000?00(01)?000
0?000??0000???300?0??????0??00????1??2000100000000??0000?00?00
?0??0??000???????01?0?????0?0?????????1
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Shuvuuia deserti

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?01101000000007112011000?0?0?0?111?1100210000101010010010???1?1
000010100000210O?10211??000??0111111011101?0??1?2010120121101O0
?1000?00020003011??1122011000?1??011?2000?0?10021032?0???210100
111011211(01)000300000011000001100000010000?00??000000000001?01
00?00000?0000?10010000000??101?00??1??00110?01?1000??0(12)0????
0100?0010000?0?0220?0??0?????20?10?000?0100000111??0001000?00(0
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1)?0000?000????????300?0??000??00?0?0?001002000100000000?0000
000?00000000?00000100000?01?1010001????????1

Patagonykus puertai
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??????????????????????????????1?011?111???(01)12(01)10?2???
???????????00200??0110???????1????1????1??0?????10????21101??
1100?000100001110??0????0?1??0?0?1???00????????0010?0??????????
??????????????????0??
???0?0010?????????????????????20?00?00??01??????0?0?000???0?00??
??????????????????0??????????0???0????10120000000000??00??????
???00??0?????????????????????0??????????

Albinykus baatar
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????????????????????????????1?????????????????????????????????
?1101???11100300000?????????????????0000?????????????????????
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????????????????????0?????0???????0100001O0?0000000??0??0
????00????????0?????????????????11

Alvarezsaurus calvoi
??
????????????????????????????100????????0?2?10?2?12??????
??????0?0?00?????????0????00011??0??2?????????????????1?00??
?0??0??10000000???0????????1???0????00???????0?????????????????
??????0?????(12)??
??0?12???00?????????????????2?????????0?0?0?????????????????????
?????????????????????????0??0?0?001??2????0000000?????????????
???0????????????????????????????????0

Proceratosaurus bradleyi
??1?0?????????????000101011100O0?00??????????0???000?????????
?000?0000?00??000000001010111?????????????????????????????????
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??????????????????00??0????0?0?????????????0000001O?1?00?00
?00????0?2?????00?000???0???????00?????????0?????0?????00???
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??????????????????0?????????????

Ornitholestes hermann
?0100???0?0?00?1???0?010?01110001?100001?0??10000000?01011????
0000001000?0?000010?00101001????011?0101110000??000?0010??1???
???????????01?00?????????00001??1?0?0(01)00100000001??0?1????
???0????????00?00????00000?0010?00?0?0000?0?0000?0000000??01?0?
?0000000?0002?11100000000?0???000000?0?00???000000000???0000
000010000(01)0?????????????????????????????0?0?0010000?0000
00000000??0??0????1000??0?00?00?000?00000?0000????????0000?000
?000??00?0?????0?000??0???0001?0?????????0

Coelurus fragilis
??
??????????????????????????0??0100100001110O0?????0?000???????
??????0?0??0?10001??0??0?????????????????????????01100?000000?
0?0?00110?0?0????0?00??00???0?????????0?0?0????0????????????????
??????????11100???0
01000?????????????????2?????????????00?0?0010000?0000000000
00010000???0????0???0000?????????002000000000000??000?????????
?0000?????????0?????0?????????0

Archaeopteryx lithographica
101?0000??000??112010010??1110?011000012100?10?0000?0??100111?0
?000001000002?00000200??00100?1?1???00?0??1?0?0???00210122110O0
????10111111110O0?1100000000112111010?1100301012102l?212?111100

000?0001000000030?000000000011000000??00?0001100100000010012?01000
000???0000?020000?00000000??00110??00?0??000?00??000???00?00000
0000(01)000?0????????00000?0000?000000000000000?0011000?000??00
0?0000100000??00000?000000000000?0?00000000?00?0?(01)1000000?00
???000001000010100000010111012?01011002?1000

Avimimus portentosus

?01?0???10011?00??0??1?1???????1???1????00?11??0?00100110?????
?2?1???00?0??0111?????????????0110101101012?1?00??100???????????
???????????0100??????????00?211?01??0101201010?010?0?1000100?
0???0001111002???00??0?0?01?02?000000?0?001000????????0??????
??00??01??0?01001?????????????????????0??0????00?00?????????020
01000?????????????????????????????0?????0?0?0010000?000000000?
??????????2??????????(02)0?000?0000020?0100000000000000??00?01
??0??????0?????????????????????????

Confuciusornis sanctus

10110?????????????1?000?00??0001???0??2??0??0??010???01??????
0000100002102001?1????????0?????????1011?0?2???0?2????3??111
?11010??13111000?1111100000011212?1?1??11000?1?111022?21?12??10?
?11??120211010030?000000000110200??00?0101??11?000011001??????
0??????000?122001(01)00110?????????10??00??011200??01(12)01111
1000000110000100100012000?00?0000?0??0??000000000?000211??0010
0000000101021010 11(01)?10?000000101000000000101010010001100011
000?00?0000(01)000???100000110111 0?00??1100?10?0

Struthiomimus altus

?01010?110??0??10102100010111012110000000000000000010??0001?01?
?000100000102000 1?1????????001?10110000101000101000000000100100
1?????0112000200000002?00001111111012111000 0?0?001000000000001?????
000100010000020??000011111110121110000?0?0010000000000001??????
00????0000??2110????0?????????????0?0?1????000?????0?00??00?000
0?0000(01)0?0?????????????20??0?0?000?0001101?0?0010000??000000
00000??0???0??00000??000000000000000200?000000000000??00?02
0000000?1002??0??00????0?00?00?????????

Gallimimus bullatus

?01010?11011010101021000101 1?01?1100000000000000001000000001?010
0000000000102000 1?1????????001110110000101000 1?100000000100100
??????0112000200000?0?10100100000011000010100100000010010000011
000100010000020??000011111110121110000?0?0010000000000001??????
00100?0000002110 00?0000(01)0010000000?0000???000000010200??1000
000010000(01)0?0?????????????20?00?000000001100 1?0?0010000?0000
000?0?000?0???1??00000??000002 0?0?0?000002000000000000001000?000
?01000000??1002??0000??0??00000?0????????0

Garudimimus brevipes

?010?????01101?????2?0001010100 0??000?00?00?0?000?????0001??1?
0??0??0??0?02?0?1?1?????????????????????????1???1??0????????????
??????????????????????????????0?0???1???0?0?????????0??0?1???????
0???????000000000?0??01??1?1??2?1?0?00?0?0??0001000000000??????
?0000?0000010???00?0000?001?000000?0000??000001011000 0??0000000
010000???0???
??????????????????????00?000000000200000001000000000003?010?0
????0000???000???0??001000????????00

Pelecanimimus polydon

?01???????1????????2?00????100?????????0??0?????????????????????
??00?0000??????000211??0001?????????????????????????????????????
?0?00????2????00??00?1010?????????????????????????????????????
??????????????????????001110????0?????0?????0????000?0??0?1?0????
???????00?0?0?10???0?0?????????????0?0?????????????????????0?????
??0?????????????????????0????0?0?0?????????????????????????????
????????1??0000???00000?????????????????????????????????????0?
?000?????????????0?????0??0??????????

Harpymimus okladnikovi
?0?????????????????2?0???
??0??00?00?????????200??1?????????????????????0?????????????????
???????????????2?000000000?10?10??0???????010?????00????0?????????
????????0000000???0?001011????1?0???00?0?0?0???000??0000??1?0????
??????000??11?10000000?????????????0?????????????0000??00?0000
0?0000(01)0?????????????????????????????00??01?0?0010000?0000000
00000???1?010?000000?0000000?0?0000?00?????00000000?00000?00??0
0??0000?1????????00?????000??????????

Troodon formosus
???1?1112?11010000001???0?011?0??????2022000021O?00?1?01100????0
?10??001?????????0111010100???1111100101111111?1000?1020??11??
??????????1?010????0?000010?????????0?0?2?10?11000?0??0111100
0???00010000021??01???000??1?0??010???1??0??0?0?00000?0?0?????
??00?????????????????????????001??0?000?????0??1?1?????????00???
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??0?
????00000101001??0???1110?1?????????

Saurornithoides mongoliensis
?01??1?1??1101???0?110001?1000????????2?????????????????1?010
?100?0010??1????0001110101?????????1???0??1?????100??1?????????
??????????????????????????????????0101201O?010??10?1?11110?
??????????0???10?01??????0??1?0?????????010??00000??0?1?01?0?
????0??000??????0??0000?????0?1000?0??0??????????0000???0????0
0100?0???
??????????????????????00????????0?0????000000000000020?02000
00000000101001?10???1110?1?????????

Zanabazar junior
?01101?12?110100?001?000??100000????2022000?21??0????11100?????
?100?001???1????0001110101001?????????1???0??1?????100??1?????????
??????????????????????????????????1?????????????????????
??????011????2??????????00??00???11???????0??000000000100000?
???1???00???????00?000??????001??0?00?????????????0000??0?00???
?????0(01)0???
??????????????????????????????????????00010000??000??2????
0??0???00000101001?11???1110?1?????????

Xixiasaurus henanensis
?????????????????????0100010111O??????2?22?????????????????????0
?00??001????????000201??01?0?????????????????????????????????????
??????????????????????00?1?????????????????????????????????????
??????????????????????0???00?????????????????????0?000000???01?00
00?????00??????000000???00?????????????????????????0?????????
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???????????0??????0???
?0?0?????????????????????????????

Byronosaurus jaffei
?????101???101?1100110001011?0??????2022O?????????????1?100?????
?0000001??11???000211??01?0?0???????010111????????0??02???????
??1????
0?0??0???????21?????????0????0????1??????????00000000?1?00???
?0??00?000??0???000000?????????????0?????????????0?0????0????0
010???
??????????????????????????????????000?????????????????????????
??????000100011??0????????1?????????

Sinornithoides youngi
?0??01?????????????1?000??1??0????00???2???????1?0?????????????
?00??0010??????0001110?01??????11??001?????????0011?10112101
????1?00?1?101?0???1000000????21??01??01??30???11?0??001??1110?
????0???1?000110001?0??0?0?1??00?0???0???0010?0??00000????0??0?
?0????00???0?1000000?0?????????????????????00?????1?00??000????
??????(01)0?0????????0??0?20??0?00000?0??1000???0?1000???00?0??

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???????0??010?0000???000000??00??0??000???000000000000000020?02
000000000?????????101?????1?010100??1??
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Sinovenator changii

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?0???0002?000011110010101?1110?011?02??2??0011???011?10100????0
?000?001?????000001111O?1?????11?10100011110?00100011022l?1???
??????110111?????????1000?0???0?211?010111(02)0301?1110211201?111
10000??100110001l1??110?000000???000011000100011000000??1??011
??0000?000000??0??000000000000??000000?00?0??0000010100(12)00??0
0000?00100000?????????????????20000??00?0100?10?????????????????
??????????????????????????????00?100000010000000000000?0?00?020
?0100?000000000100010?10??1011000???????00
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Mei long

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?0????????0????????11010?????0?11?00201210000l?10?110??100?????
?000100l0??1?0000?021???01?001101110001l?1110?01???0110221111?1
1????111?11100?0?1?10000001?012111?1??1100301?1110211???0111100
?01010010000??110011?0?0000???00000??000100?1??0?0?000000?001?0?
0000??000001010000?000?????????00?0??0??00??0101????????0?0000
010000(01)0?0????????0100020?00?00000?0011000?0?0000000?0000000
?000?01?1?0???00000????00000?000000100000??000000000000?000021?01
000000??0???100??1010??101100?1100?10?0
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IGM 100/44 EK troodontid

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?????0012?????????????????????????????????????????????1??0????????
???????1??11?????????1?????0?????????????????????????????????????
??????????????????10?00000?????????????????????????????????????????
??????????01?1?001???00??????0?0??1?????????0?????????????????????
????????????????????????????????????????????????1?1?????????????
????????????????????????????????????????????????????????????????
????????????????????????????????????????????????????????????????
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Jinfengopteryx elegans

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?0?????????????????1?01???2000????????1??00?0????01????100?????
?00?00??0??1??0?000?1???0???1?????????????????02????1?200?
1?????1101110??????1000000?????1?????????????????2??0?????????
?0?????????????????0?0??00????00?????????????00?000001???0??0?
0???????0????100?0?000?????????????????????????0??????0?000?
??0?0??0?0?0?????????????00?0???0?0?00???0?????????????????????
????????????????????????????????????????????????????????????00?
0000?????????????0??11?01????????????
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IGM 100/1126

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?0????002?0000?11(12)01?010??2000?011?02012100011O?0?10010100??
0??000000000?11?000000211??00?0?????????????????0????01102????
?????????????????????0??10000001???211?010?0100201000101210l2??11
1000????0??2?00121000l?00000011?00?0?020000?00100?0000000111?01
?0?00?0000003??????000000??????00??00?00?0??0??0000000?00???0?0
?????????0?????????????????????????????????????????????????????
???????0?00???0000???0100000?00??0???0?00?00????00?1?000?20?02
????000000101001l1??0??101?001???????0?
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IGM 100/1323

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?01???????0???11???1?000??20000?1??020121?00?1??0???0?????00?0
?000?0????1??00000021???0000?????????????????????011?????????
??????????????????????????00??1??????010?20100(12)102?1011????
???00???0????0??2???01??00??0????0?0???00?0?00100?00000000?1?01
?0?00?000?003?????0000000????00?000?00?0????000000?000??0?00
????????????????????????????????????????????????????????????????
??????????????????????????00?????00?00?0?00?????????1000??2????
?????????????????????????01????????????
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Anchiornis huxleyi

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001100?????????????11010??11100????0?2?000??1????1?1??????????
?000??01??1????00020???01??0?101???00?0??010?01???011012l0??01
1????011111110000??100000010?21?10011010?201?1?112112????1?1?0
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00??1?01?000121100010?1000?1??00?0???????0?11?00?000001???0??00
??????000???020000?000?????????????0??????0????0??????0??????0000
0?0000(01)0?0???????00000200000?0?00??0?10000?????10?0???0?????
??????????10?01000??0?00?00??00?00000?????????????00000?0?00??0
0000000000????????00??1110?1?1?1100010??

Xiaotingia zhengi
?01?????????????????1?1???111000????0?2??????????01?1?????????
??0010012?1???00??020???01??0??0???1?0?????10?01?????1??????10?
1????01?01111?10???10000001011?1110?1101122?????102?12?????????
??10?????????1?0100010100000?1??0?10??00???0010?000000??1???00??0
?????00?0???210000??000?????????????????????0000?????????0??000
?10000???0????????010002???????????01?000?0?00???0???0?0?0????
0??????????01000?1?00000???0?0000?????????????????????0??0?02???
?10000????????00??1??????1?1100?10??

Segnosaurus galbinensis
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??1??10?0000?000???0100000?????????????????????1???0??????????
????????11???00????????010?20021?0000?1100211?0?1020?0?????????
00??0?000?0000?21?0??00????1??0?0???00?0?00??0?????????????????
????0?????????0?????????????0?????????????????????0?0????0??????
??????????????????????0??????0????00?????????????????????????
??????????????????????00??000???10?????00??0??000000000??2??0
????00?????????????????????0??????????

Erlikosaurus andrewsi
?0110??02?0?1?0??1010011100??0001?100001000010000?0??00000??111
121001000000200017001000001?????????????????????????????????????
????????????0???
?????????0?00?0??????00??01??00?0?00?????????0?00001010010??
??0000?000????0?000000000011???10?0100???000000000000??0000???
??????????????????????????????????????0?0010000?001000?000
??0???0000??0???
??0000?0????000???0?000?0???????????

Alxasaurus elesitaiensis
??
?210?100???????????100?001?????????0?01010000?1?000??02?0?1??
??????????00000?100?0000120021?00?01010?211?021?2?????01????
00????????000002100000??00??1??00?0??00?0?00??00?????????????
???????????0????0?????????????????????????????????0??00????0
??00??(01)0?????????????????0????????0??00?????????0?0???0?????
??????????????0000???000?????????????????????????????????????
0000000?0????0???0??????????0??????????

Tyrannosaurus rex
?10000?0110000100210000010101000000011010010211000010010001?000
0000001001100100000000010101101000000?0000101000000100000?001000??
1?????000000010000??0??100010310001000000001011011000000?010010
000?000100000200000001000000000000000?0?00101001000000011000?01
111101111210201100000000000000000?0000??000001011000??0000000
011000(01)0?0???????000002001?00000100011?0?0010000?0000000
00000010??0????000???00??00?000000000210000000000000000000?00
000000??02000??0001?0??00100000110?0000

Tarbosaurus baatar
??????????????????0?????????????????????1????????????????????
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??????????????????0??
???????????????2????????????????????????????????0?????????????1
11110111112??2011000000000??00?????0000???000?????????????00???
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000??02000??0001?0??00100000???????0

Albertosaurus sacrophagus

?1000??00?0000?002?0?00010??100?0000110100?021?0??0?00?00000000
?0???????0?1???000000001010111?????0????001?10??0????000??0??????
??????000000010000????0100010310001000000010110110000002?0?00?0
000??001000002000000010000000000002?000?0?0010?00100000011000?00
1111011112102011000000002??000000000002??00000101??000???000000
0??00??0?0??????????????0?20010?000001000110?0?0010000?0000000000
00010??0?????000???00??00?000000000210000000000000000?00??0000
000??02000??000??0??00100000110?00?0

Gorgosaurus libratus

?10000?00?0000??0?10000010101000000011010?021100?010010000000?0
000000100?100100000000101011010000??000101000000100000001000?
1000100000000100000000?0100010310001000000010110110000001001000
000?000100000200000001000000000000?000?0?00100001000000011000?00
11110111121?2011000000000?000000000000???00001???0000???000000
0??00??0?0??????????????002001O?000001000110?0?0010000?0000000000
00010??0?????000???00??00?000000000210000000000000000?00??0000
000??02000??000??0??00100000110?00?0

Daspletosaurus

?11000?00000001002?000001010100000?0011010010211000010010001000
0000001100?100000000000101011O???000???001?10??0????000??0??????
??????000000010000????0100010310001000000010110110000001001000
000??00100000200000001000000000000?0?0010?00100000011000?01
11110111121?2011000000000???000000000000???00001?1?0000??0000000
0??00??0?0??????????????002001O?000001000110?0?0010000?0000000000
00010??0?????000???00??00?000000000210000000000000000?00??0000
000??02000??0001?0??00100000110?00?0

Eotyrannus lengi

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?00??010???????000000101O?1?????????????????????????????????????
??????000000001?0?0???
?????0????0??????0???0?00???00?0????0?????????00??0??00??0?
11?????10?????1?0000?????????????????????0??0?000000???00??????000
??????????????????????????0000?0?????000?0?0?????1000???000000???
??01?????????00???0?
?????????????????????????????????

Dilong paradoxus

?0100??0000000?100100010??101000010011010000100000010?0000?????
?0000000??00?000000000101011100O1?0?0100??1?0??????0??012(01)0?
????????????000000110O0????0000?00001??10??00101O0?0?0?0100000000
00?00??00010?00100?0000?00000?0?00000?000?0?00100000000000011100
?000111???0000101O?000000??????0000?0?000???000001?100000???000
??00?000????0?????????????20?00?0?0?00000100O?0?0?1000???000000
000??0?0??0????1000??0000000???0?00?002000000000000000000?????00
0000?0000?0?10000???0100000000?????????0

Shenzhousaurus orientalis

???0?????????????????21000l?1000??1???000??00?000?00?????????????0
?00000000??0??0?1?12?0??1?????????????0????1???0???00000??(012)0
??????????????????????????00100000001??110?0000100?000000100??00
001?0?????????????????????0??1??1?0011?????00???0010??000000010???
?????0??0??00???0???00?000?????????????????????00?????0??????0?
00?0?100?0?0?0???
??????????????0?????0?00000?00000?0002?000?????????????????????
??????00?????????????????00?00?????????

Ornithomimus edmonticus

?01010?110?101?10102100010101010110000000000000000010000000?????
?000000000l0?1001?1??????0?001?10110000101000101000000000100100
1?????0112000200000000?10200100000011000010100100000010010000011
000100010000020??00?011111110121110000?0?00100010000000001?????0
?0100?00000001100?00000?????????0?0?10???0000000?0??????000000
010000(01)0?0?????????????0??0?0?0?0?00?1001?0?00?000???000000

0??00??????1??00000??000002O?000?00000200000000000?0??0?????0?
?0??000?1???????0???0??0000000????????0

Archaeornithomimus asiaticus

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??????????????????????????00?10110000101000?100000000?0????
??????01?200?20000?00100(12)0???000?1100001010002?002001001000001
1?000100010000002?0?00001?11??10??1?1??00?00?001000?????????????
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0?001000?(01)0??????????????????20?00?00000?0?1??01?0?0010000?0000
000000000?0000???0?0000??00??00?????00?002000000000000?0000??00
?0?00?000?????????????0??????0???????????

Anserimimus planinychus

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??0?????????????????0???
???????1???0?2????000?10200100000011000010100???000?001???????
????????00002???00????11??10??1?1??00?0?001000?????????????????
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????????????????????0????????0??0????????????????????????????
??????????010000?00000?????????????????????????10000??02??0??0
??00?1?????????????????????????????

Huaxiagnathus orientalis

?01?0????????????????0001???1???0?????00??0????????????????????
?00?0010???????000010?1010?00??0???1????????0??????00???0210001
0????000000000?00??001000000020?0??000000100?000011?0???0?????
?0??0?010000000?0?011??000????00?0??00?0?0010?00000000???1?00???
?0?????000???100???0000?????????00?????????????????????00?00
?1??0?(01)0?0????????00000020??0?0?0?0?000100??????10?0???0?????
????????????010????000??00?0???00000?????000?0??00??0??0????
000000000???????000????00000?0?00??100

Sinosauropteryx prima

001?0????????????????0001???1???0?????0000?????00??110??????????
?00??01?????????0001001010?00??01??100????1?0?0????00?110010001
0?????000000000?10??0010000?00020?????0000100?000?11?0?1?00?0??
000?0?0100000000?011??0000??000?0??00?0?000??000000000??1?00?00
??????000????10000?000?????????????0?0???????0101????????0000?0
??0?00(01)0?0?????????????0??0?0?00???0??00???????0?0???00?00?
??????????1??0000???0000000?0?000??0?2?????00??0??00??00?0???0
000000000?????????000?10???000?????????0

Compsognathus longipes

?01?0????????????????0010??1??00?0?00000????011???0??000????0???
?00000100?1?00?0000100101010007?01??00(01)0???1?0?0???000?010110
001??????0?000000?10???0???00?00?????????0000100?000?01?0??????
???00?0001000000000001100?00????0?0???00?0?001000000000001?00
000000?00?000?1010000?0000??0?00??0?0????0???0000?????1?0??0000
000?10000(01)0?0????????00?0?20??0?0?0?0?00?100????0?1000???0??
??0????????????000????0?0??00????000?00??????00??0??000?00000
?000000000000????????0????000000????????00

Juravenator starki

?011?????????????00000??11000????00021?0?00?0??????00??????
?00000100???0????0001001012??00??0?????????0??????00??100?0?01
????00?000000000???0?000000000?01100?????????????????0?0???
00??????1?0??000000?10?000?1??0??0??00?0?????000000000?1?00?0?
000???0000???11000?000?????????0?????????????????0?????000?00
???00??0?0?????????000002??00??????000100000?0010000??000?000?0
00???0?0????100???0000????00?000??2??00??????000??0?00?0?00000
000000?????????00??????0?0000000?10?0

Jeholornis prima

10????0????????1???0???0?????001?????????????????10?????????
?0000?1???00?00?1?1?????????0????????0????1?0?11???02111021??01
?0???01103111000l??1000001011?1??0??01?0???1???1?211?10???????

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01????0101101003000000000??0??1000??00?010????1???000?1?????0??
?0??0???0??12200?10010?????????????????????0????00000000??00?0000
00100000?0??001???0000?00000?0?1000110001000?0010000?000?0000?0
000100001011000?000000000000?00000?0100000000010000010000?00000
001100????????011?1110???1?1100?10?0
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Jixiangornis orientalis

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101?????????????????0010????001????0?0??00000???????0100?????
?000001????0?0??1??0????????00?0???1?00????1??20???02??1021??11
?1?000110311100011010000001111210101021100001010?211?10?2?11?0
01??1?01(12)1101003000?00?000?0??1000??00?0100??110?001?1??????
???00?00?0000?12200?00010?????????????????????0????000??00?0
000?11?0?10?11?0????2000000000?00100111100102?0?0000000?000???0
??0????0??010?00100??0000?00100000010??0000??00000100000?00?00
00?001100????????00??11????01?1100?10?0
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Yanornis martini

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?01?????????????????1?010????0?11???0??2??0???????0?0?????????
?0000011???0????000?1???00??0????1???0????????4?1???????03?????
?110?011031110?011?113001020????????????????????????22?010?2??10?
?1??0?0121(23)0000300000??0001???00?0???????0???21?0?0?????????
????????????????2001000111???????????10???????1?????????????????
0?0011?00???0210?(12)??10100001010?1?11?111100111??0101?0101?10
000?0?????021(01)101311(01)1100(01)100?0?1?0??0?00??????0??00?1
110(01)?1?00??1?0??01100????????01??1????????1100?11??
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Apsaravis ukhaana

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?????????????????????????0????????????????????????????????????????
?0002?1?0??0?????????????????1??11??10200??1???5?10002?1??23?????
?1?0101103110000111113003??000?1???1?200000?1?021?222O??12?010?
????1??12130100?00000??20???1?20?0?????0?00??21?????????????????
????????????200?10?????????????????????0?1(01)?????1?0???????
?20010?(01)001??21??1???????00000?0?10001110111117?01011010(12)
011111000010102111O?(23)120100?11??20?1(01)0010111?110?10121121
11111?0000?1?0??01101????????011??????0?1????????00
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Yixianornis grabaui

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101??????2?021??1?????0?01????0?1?1?0????????????1????0100?????
?000?010???0?00?00120???10?01???1???0000??1?0?40??0???0023???11
?110001103111O?0010113000010002171?01?2110030100010222??0211?0?
?1??????213010010000??000?0??1000?20??0?000001?????????????0??0?
?0????0??0?122001000?????????01??1????????11(01)?????1?0?????10
?20011000?11021??(12)??10100001010?1111011110011110O?0110???01?
000???0?01021(01)10?31201100(01)100?00100?00?002?101?????11110
(01)?1?00??1?0?001100?????00011?11?01????0100?10??
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Sapeornis chaoyangensis

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?011?????????????????0?010??11000????00??21?0?00??????0??????0???
?0000010??10?0000002O??????00????1???000????0?211??0210003??100
?????2110111101001110000001011217?00?211000?101(01)00211210????
1??01??1001210?100300000000000????2000??0??0100??0100?000???1???
00??0???00000??2200000000??????????????????????????0?00???000
00000100001007????????000002O000?00000?00000100O?0?01010?0010000
?0???010?1(01)10?11100??0(01)00?0000?0000000?000??00?00??000001
?00??0?00001000????????001?1?1011?1?110001000
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Neuquenornis volans

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???????12????????20?????????????????????????00??????00????????
?????????????????????????????????????????00?????????????????????1
?11011?1031110?011111000?????????????????????????????????????010?
??????????(01)01003O??0????0??????0?00???????????1????????????
??????0????????0100?????????????????????????????????????????????
??0110?????????21????10110??0100?001?001?0??(12)??1???01?0???0??
???(01)?????????2???20?1??01?????????????????10?1????????1?0???1
011???????0?000???10000011O?????????????????
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Patagopteryx deferrariisi
?0??????????????????????????????????????0010?????????????????
????????????????????????????????????2?????????????????????????
?????????????0?1???????????211101?????????????????????2?0100
01??10012130100l?000???????1????????00?0?????1?????????????????
??????0?????0?????????????????00?1?????00??111110000?????????010
000000???????0????????000????0101?1110(01)00???(01)?10?0???010
00001(01)0001?(12)00???30???????00?2000000?010120????0?000(12)1
1001100000?(01)?0??0?100?1?100??01?0???0?001????????00

Cathayornis yandica
?0?????????????????1?010?????0?1??????????0?????????????????
?00????????????00001???????0????????(02)????????3?????2????3??
?0??11?02?1031110?011?11300?0?01111?0?00?11000?101?102122??????
????1???0??(12)1(01)1?0?3000?0???00????0??1??0??0100???100?????
????0??0????????????2200(01)0?011?????????????????????????0??
????0????0111??0010?20??1??10110?101????010?0110001001011O(01)?01
020111110?(01)?1?????210120?11?01?0101011?0?000001???1?0?0?1(01)1
?0??????????0??01110????????01????????01??????????

Concornis lacustris
??
????????????????????????????????????00?????????????????????0?
?11?02?1031110?0?1??1?0030???????????110?101??11?222???0???1??
?1???0?1(02)11??0?3000?0???0??????????????001??1?????????????
????????????????2200???
??0111????10?20??1?0101100101?0?0010001?0??(01)001?110??0102?1?
??10???1(01)1?(12)?????????????(01)???????????00?????0?100??1
?00??1?(01)1??0??????110?????????????????????1100110??

Gobipteryx minuta
?0?????????????????1?01010?0?0?????????????????????????????11
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Vorona berivotrensis
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Songlingornis linghensis
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Pengornis houi
?0110?????????????1001O??0?00??????0?12??0???????0??????0?????
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?1?????211???0?000??0??000???0??0??00???0???11?0?000??????????
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011??00100????????01{01}00?00??????0??1??012111{01}0?011010001

{01}{01}1?????1??1???10{12}{12}0??1??1?11??????0????00?0????0?
?0{01}?1?00??1?11??0?0??0?100????????01????00?01?1001011??

Hesperornis regalis
?0?????????????????00010100?00?????00021?001????00?0???00????1
?000?001???1?0001?021???00??10101110?2100??11?50100?210?23??11?
?10??00103111???????????3??0202100?1??00000???0210222O??12???00
01??11?1213110010??0?00??01?1?0000?000???00??2??0?1111????0????
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011000012?0?0001001O0?0???10?0???00001??0?????????0???0????0???
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Baptornis advenus
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Ichthyornis dispar
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?100?00103111O?0111113003??0102?1??10211000????210222???12??100
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Iaceornis marshi
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?1101?010311?????1113?03?????????????????????????????2??1??
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Limenavis patagonicus
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0101010011?11(12)313011?011?????????????????????????????????????
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Crypturellus undullatus
10????012?020002?2001010100?00?111?12002100001011110000 10???1?1
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?11010010311011011111300 3??00121000 1?2012011002102222??12?0100
0100110121301?0???01000200001?20000200?0?001021???120??01?????
0????000001020021121 11(01)0101001111101011001101111111111001010
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Lithornis
101?????????????????01010100?00?111??2?02?00?0?????????????????1
0000?00????0??101?1?????????1????????2????????(67)?1???????????
?(12)??1100001031111001 1?113003??00021010 1?20100101??2102?????1

2?01000???11?12130100?????0??200?01?2010???0?0?0???21???12?????
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?01?10121012?0111(12)12111221101002?0101101111011110111110011000
1(12)1110000101010101111113130110(01)11102(01)01201101112110201
10002111122210010(01)?000011?1???????011?111??00??????????

Gallus gallus
101???102?021002?2000010100?00?111?120021?0001?10100000?????1?1
0010000000000?1101?1?????????101(01)1111221?0?01007?120??12?23??
1(12)1?11012010311020011111300 3??0012111112?2?10011100210222??1
2?0100011011??2130100100010002001002010020 0?0?0???21???121??01
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0111210101120111211112110100021011111111111110011111011000120110
0001011101011111131401001211021?12111111121102021100211113222 00
111?00?011000101000001111112000??00101102?

Crax
10110112?2?021000??0010101001?00?111?12002100001110100000100??1?1
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?1100201031112101111130 03??0002100?1?2?10011100210222 0??12?0100
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0101120111211112110100021011111111111110011111011000120110000101
1101011111131401011211021?111111111211020211002111132220011000 0
0011000?0100000111111000 0?11100011??

Anas platyrhynchus
101???102?021002?2101001100?00?111?10002??00?1?10100010?0???1?1
020000010 0?011101?1?????????101?1111221?0?011?7?11???10?2310121
?1101111031111101111130 03??0012000?1?2?10011100210222 1??12?0100
011011?121311?0???0100021 01?1?20100?00?0?0?1021?0?121?????????
00????000001120021021111111111122110211121111111011000111101112 1
0101020111211113120100101010?1(01)1111111000111001100012011000 0
1011101111111231401010111021?111110111111010211001100012011000 0
1011101011111231401011111021?111111111211020212002111122220010 0
0000011000101000101111110000?11101?11??

Hongshanornis longicresta
101?????????????????11010?????0?11???0????00??????1????????????
?000?001??00????1?1?10???0??0??01??1?0????????(234)??????????3?
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??0???????????1??2000??000100?0??0?0??000????????1???1100??(01)
?00??2?0???1?????????????????????????0100?11??

Liaoningornis longidigitris
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?1????0?21211003000?????0??
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??01???2?????????????????????????01?1?0??001111110201000?00???
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Pedopenna daohugouensis

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Epidendrosaurus ninchengensis

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?0?010????????00??????1???????????0?
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Epidexipteryx hui

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?00?????????????????1?????00?????0??2??0011?????????????????
??100?0?0????0000102O???10000?????????????????0?(01)????1?1?122??
10??0????0101?010?0???????00?1???????????012?????011?02?0??????
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?2?????0????????1?0?????0??????????0?????????????????????000
?0????00??0?0?????????????0??0?0??????0???0????????????00?(01)
0?????????????????????????????????????????????????10?0?0?0???
?00?00???0?????????1??11??1???????????0
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Haplocheirus sollers

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?00110??0?010????0110111011100??10??20?00???100?0???0101?0011
0000101101102?1000?011?100??00??10??0?0111101??0??0001?0??20??0?
??????100?100??110?0??00010???1???00?10010200010?011000?100000
00???0??0000000??00?11100011100?0001?0???0010?00000001000???00
000?0??000?10??00000000?????????0?????????????10??0??0??0000?00
0??00?????????????????????0?00?0?0?0?000??0??????12????000?00????
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APPENDIX 4

List of Synapomorphies from Phylogenetic Analysis

The following tree provides labeled nodes for reference of the listed synapomorphies.

Node 100:
- Char. 96: 0 → 1
- Char. 178: 0 → 1
- Char. 264: 0 → 1
- Char. 266: 0 → 1

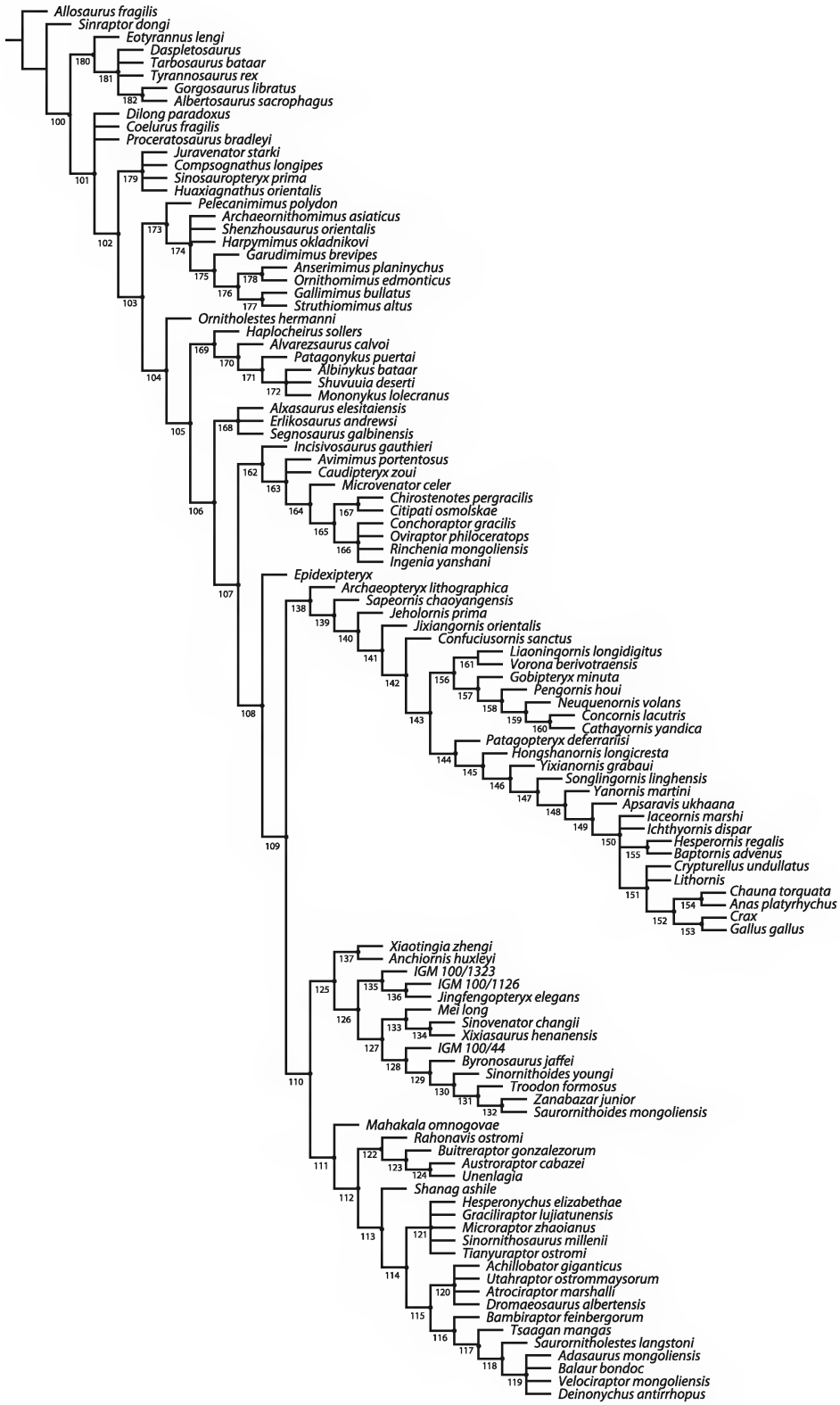
Node 101:
- No synapomorphies

Node 102:
- Char. 33: 0 → 1
- Char. 76: 0 → 2
- Char. 90: 1 → 0
- Char. 95: 0 → 1
- Char. 124: 0 → 1
- Char. 136: 0 → 2
- Char. 216: 0 → 1

Node 103:
- Char. 35: 0 → 1
- Char. 53: 0 → 1
- Char. 56: 0 → 1
- Char. 102: 0 → 1

Node 104:
- Char. 4: 0 → 1
- Char. 20: 0 → 1
- Char. 46: 0 → 1
- Char. 84: 0 → 1
- Char. 88: 1 → 0
- Char. 91: 1 → 0
- Char. 120: 0 → 2
- Char. 157: 0 → 1
- Char. 161: 1 → 0
- Char. 174: 0 → 1
- Char. 217: 0 → 1
- Char. 285: 0 → 1

Node 105:
- Char. 9: 0 → 2
- Char. 66: 0 → 1


Allosaurus fragilis
Sinraptor dongi
Eotyrannus lengi
Dasplетosaurus
Tarbosaurus bataar
Tyrannosaurus rex
Gorgosaurus libratus
Albertosaurus sacrophagus
Dilong paradoxus
Coelurus fragilis
Proceratosaurus bradleyi
Juravenator starki
Compsognathus longipes
Sinosauropteryx prima
Huaxiagnathus orientalis
Pelecanimimus polydon
Archaeornithomimus asiaticus
Shenzhousaurus orientalis
Harpymimus okladnikovi
Garudimimus brevipes
Anserimimus planinychus
Ornithomimus edmonticus
Gallimimus bullatus
Struthiomimus altus
Ornitholestes hermanni
Haplocheirus sollers
Alvarezsaurus calvoi
Patagonykus puertai
Albinykus bataar
Shuvuuia deserti
Mononykus olecranus
Alxasaurus elesitaiensis
Erlikosaurus andrewsi
Segnosaurus galbinensis
Incisivosaurus gauthieri
Avimimus portentosus
Caudipteryx zoui
Microvenator celer
Chirostenotes pergracilis
Citipati osmolskae
Conchoraptor gracilis
Oviraptor philoceratops
Rinchenia mongoliensis
Ingenia yanshani
Epidexipteryx
Archaeopteryx lithographica
Sapeornis chaoyangensis
Jeholornis prima
Jixiangornis orientalis
Confuciusornis sanctus
Liaoningornis longidigitus
Vorona berivotraensis
Gobipteryx minuta
Pengornis houi
Neuquenornis volans
Concornis lacutris
Cathayornis yandica
Patagopteryx deferrariisi
Hongshanornis longicresta
Yixianornis grabaui
Songlingornis linghensis
Yanornis martini
Apsaravis ukhaana
Iaceornis marshi
Ichthyornis dispar
Hesperornis regalis
Baptornis advenus
Crypturellus undullatus
Lithornis
Chauna torquata
Anas platyrhychus
Crax
Gallus gallus
Xiaotingia zhengi
Anchiornis huxleyi
IGM 100/1323
IGM 100/1126
Jingfengopteryx elegans
Mei long
Sinovenator changii
Xixiasaurus henanensis
IGM 100/44
Byronosaurus jaffei
Sinornithoides youngi
Troodon formosus
Zanabazar junior
Saurornithoides mongoliensis
Mahakala omnogovae
Rahonavis ostromi
Buitreraptor gonzalezorum
Austroraptor cabazei
Unenlagia
Shanag ashile
Hesperonychus elizabethae
Graciliraptor lujiatunensis
Microraptor zhaoianus
Sinornithosaurus millenii
Tianyuraptor ostromi
Achillobator giganticus
Utahraptor ostrommaysorum
Atrociraptor marshalli
Dromaeosaurus albertensis
Bambiraptor feinbergorum
Tsaagan mangas
Saurornitholestes langstoni
Adasaurus mongoliensis
Balaur bondoc
Velociraptor mongoliensis
Deinonychus antirrhopus

Char. 136: 2 → 1
Char. 153: 0 → 1
Char. 157: 1 → 2
Char. 166: 0 → 1
Node 106:
Char. 35: 1 → 0
Char. 40: 1 → 2
Char. 45: 0 → 1
Char. 76: 2 → 1
Char. 107: 0 → 1
Char. 146: 0 → 1
Char. 216: 1 → 0
Node 107:
Char. 9: 2 → 1
Char. 20: 1 → 0
Char. 57: 0 → 1
Char. 68: 0 → 1
Char. 79: 0 → 1
Char. 303: 0 → 1
Node 108:
Char. 84: 1 → 0
Char. 134: 0 → 1
Char. 139: 0 → 1
Char. 198: 0 → 1
Char. 464: 0 → 1
Node 109:
Char. 66: 1 → 0
Char. 133: 0 → 1
Char. 138: 0 → 1
Node 110:
Char. 39: 0 → 2
Char. 61: 1 → 0
Char. 71: 0 → 1
Char. 74: 0 → 1
Char. 75: 0 → 1
Char. 109: 0 → 1
Char. 204: 0 → 1
Char. 384: 0 → 1
Node 111:
Char. 17: 1 → 0
Char. 56: 1 → 0
Char. 58: 0 → 1
Char. 88: 0 → 1
Char. 96: 1 → 0
Char. 103: 0 → 1
Char. 201: 0 → 1
Char. 452: 0 → 1
Node 112:
Char. 113: 0 → 1
Char. 464: 1 → 0
Node 113:
Char. 83: 2 → 1
Char. 237: 0 → 1
Node 114:
Char. 29: 0 → 1
Char. 71: 1 → 0
Node 115:
Char. 20: 1 → 2
Char. 43: 0 → 1
Char. 44: 0 → 1
Char. 73: 0 → 1
Char. 97: 1 → 0
Char. 228: 0 → 1
Char. 317: 1 → 0
Char. 354: 0 → 1
Char. 450: 0 → 1
Node 116:
Char. 10: 0 → 1
Char. 16: 1 → 2
Char. 265: 0 → 2
Node 117:
Char. 19: 0 → 1
Node 118:
Char. 60: 0 → 1
Char. 251: 0 → 1
Node 119:
Char. 207: 0 → 1
Node 120:
Char. 83: 1 → 0
Char. 91: 0 → 1
Char. 238: 0 → 1
Node 121:
Char. 165: 0 → 1
Char. 232: 0 → 1
Char. 440: 0 → 1
Char. 443: 0 → 1
Node 122:
Char. 157: 2 → 1
Char. 163: 0 → 1
Char. 165: 0 → 1
Char. 177: 2 → 1
Char. 226: 0 → 1
Node 123:
Char. 203: 0 → 1
Char. 227: 0 → 1
Char. 229: 0 → 1
Char. 317: 1 → 0
Char. 339: 2 → 1
Node 124:
Char. 108: 0 → 1
Char. 198: 1 → 0
Char. 265: 0 → 1/2
Node 125:
Char. 21: 0 → 1
Char. 51: 0 → 1
Char. 203: 0 → 2
Node 126:
Char. 37: 0 → 2
Char. 53: 1 → 0
Char. 84: 0 → 1
Char. 119: 1 → 2
Char. 139: 1 → 0
Char. 208: 0 → 1
Char. 434: 0 → 2
Char. 456: 0 → 1
Node 127:
Char. 224: 0 → 1
Char. 229: 0 → 1
Char. 299: 0 → 1
Char. 301: 0 → 1
Node 128:
Char. 8: 0 → 1
Node 129:
Char. 468: 0 → 1
Node 130:
Char. 83: 2 → 1

Node 131:
Char. 65: 0 → 1
Node 132:
Char. 28: 1 → 0
Node 133:
Char. 99: 1 → 0
Char. 165: 0 → 1
Char. 203: 2 → 1
Char. 207: 0 → 1
Node 134:
Char. 20: 1 → 0
Node 135:
Char. 27: 1 → 2
Char. 28: 1 → 0
Char. 39: 2 → 1
Char. 173: 1 → 0
Char. 181: 0 → 1
Char. 262: 0 → 3
Char. 428: 0 → 1
Node 136:
Char. 244: 0 → 1
Node 137:
Char. 29: 0 → 1
Char. 163: 0 → 1
Char. 205: 0 → 1
Char. 209: 0 → 1
Char. 244: 0 → 1
Node 138:
Char. 1: 0 → 1
Char. 18: 1 → 2
Char. 46: 1 → 0
Char. 53: 1 → 0
Char. 155: 0 → 1
Char. 165: 0 → 1
Char. 181: 0 → 1
Char. 205: 0 → 3
Char. 236: 0 → 1
Char. 243: 0 → 1
Char. 266: 1 → 2
Char. 283: 0 → 1
Char. 284: 0 → 1
Char. 317: 1 → 0
Char. 426: 0 → 1
Char. 444: 0 → 1
Node 139:
Char. 45: 1 → 0
Char. 110: 0 → 1/2
Char. 120: 2 → 0
Char. 169: 2 → 0
Char. 191: 0 → 1
Char. 194: 0 → 1
Char. 199: 0 → 1
Char. 230: 0 → 1
Char. 265: 0 → 2
Char. 318: 0 → 1
Char. 356: 0 → 1
Char. 390: 0 → 1
Char. 432: 0 → 1
Node 140:
Char. 80: 0 → 1
Char. 82: 0 → 1
Char. 136: 1 → 3
Char. 143: 0 → 1
Char. 200: 0 → 1
Char. 273: 0 → 1
Char. 339: 2 → 0
Char. 347: 0 → 1
Char. 351: 0 → 1
Char. 352: 0 → 1
Char. 445: 0 → 1
Node 141:
Char. 111: 1 → 0
Char. 125: 0 → 1
Char. 128: 0 → 1
Char. 317: 0 → 1
Char. 404: 0 → 1
Node 142:
Char. 70: 1 → 0
Char. 121: 2 → 3
Char. 178: 1 → 2
Char. 306: 0 → 1
Char. 309: 0 → 1
Char. 323: 0 → 1
Char. 365: 0 → 1
Char. 371: 0 → 1
Char. 402: 0 → 1
Char. 418: 0 → 1
Char. 425: 0 → 1
Char. 431: 0 → 1
Node 143:
Char. 71: 0 → 1
Char. 333: 0 → 1
Char. 335: 0 → 1
Char. 359: 0 → 1
Char. 362: 0 → 1
Char. 390: 1 → 2
Char. 394: 0 → 1
Char. 419: 0 → 1
Node 144:
Char. 45: 0 → 1
Char. 200: 1/2 → 3
Char. 205: 3 → 1
Char. 353: 0 → 1
Char. 402: 1 → 2
Char. 404: 1 → 0
Char. 414: 1 → 2
Char. 430: 0 → 1
Node 145:
Char. 340: 0 → 1
Char. 357: 0 → 1
Char. 399: 0 → 1
Char. 422: 0 → 1
Node 146:
Char. 70: 0 → 1
Char. 80: 1 → 0
Char. 155: 1 → 0
Char. 156: 1 → 0
Char. 345: 0 → 1
Char. 348: 0 → 1
Char. 391: 0 → 1
Char. 428: 0 → 1
Node 147:
Char. 82: 1 → 0
Char. 220: 1 → 0
Node 148:
Char. 84: 0 → 1
Node 149:
Char. 101: 0 → 2
Char. 110: 4 → 5
Char. 213: 0 → 2

Char. 412: 0 → 1
Char. 413: 0 → 1
Char. 429: 0 → 1
Char. 447: 0 → 1
Node 150:
Char. 190: 0 → 1
Char. 330: 1 → 2
Node 151:
Char. 141: 0 → 1
Char. 156: 0 → 1
Char. 170: 0 → 1
Char. 321: 1 → 2
Char. 349: 0 → 1
Char. 369: 1 → 0
Char. 392: 3 → 4
Char. 395: 1 → 0
Char. 396: 0 → 1
Char. 397: 0 → 1
Char. 420: 1 → 2
Node 152:
Char. 277: 0 → 1
Char. 281: 0 → 1
Char. 283: 1 → 2
Char. 284: 1 → 2
Char. 288: 0 → 1
Char. 290: 0 → 1
Char. 293: 0 → 1
Char. 294: 0 → 1
Char. 312: 0 → 1
Char. 344: 0 → 1
Char. 379: 0 → 1
Char. 403: 0 → 1
Char. 407: 0 → 1
Node 153:
Char. 113: 1 → 2
Char. 132: 0/1 → 2
Char. 140: 1 → 2
Char. 398: 1 → 2
Char. 430: 2 → 3
Char. 437: 0 → 1
Node 154:
Char. 19: 0 → 1
Char. 37: 2 → 0
Char. 54: 0 → 1
Char. 265: 0 → 1
Char. 292: 1 → 2
Char. 308: 0 → 1
Char. 331: 2 → 3
Char. 338: 0 → 1
Char. 389: 1 → 2
Node 155:
Char. 299: 1 → 0
Char. 333: 1 → 0
Char. 345: 1 → 0
Char. 350: 1 → 0
Char. 351: 1 → 0
Char. 356: 1 → 0
Char. 409: 1 → 0
Char. 435: 0 → 2
Node 156:
Char. 386: 0 → 2
Char. 424: 0 → 1
Node 157:
Char. 434: 0 → 1
Char. 435: 0 → 1
Node 158:
Char. 80: 1 → 0
Char. 82: 1 → 0
Node 159:
Char. 316: 0 → 1
Char. 341: 0 → 1
Node 160:
Char. 327: 1 → 0
Char. 446: 0 → 1
Node 161:
Char. 423: 0 → 1
Node 162:
Char. 22: 0 → 1
Char. 67: 0 → 1
Char. 68: 1 → 2
Char. 82: 0 → 1
Node 163:
Char. 32: 0 → 1
Char. 80: 0 → 1
Node 164:
Char. 113: 0 → 1
Char. 140: 1 → 0
Char. 181: 0 → 1
Char. 270: 0 → 1
Node 165:
Char. 184: 0 → 1
Char. 464: 0 → 2
Node 166:
Char. 246: 1 → 0
Node 167:
Char. 25: 0 → 1
Char. 35: 1 → 0
Char. 40: 0 → 1
Char. 41: 1 → 0
Char. 91: 0 → 1
Char. 101: 1 → 0
Char. 197: 0 → 1
Char. 233: 0 → 1
Node 168:
Char. 69: 0 → 1
Char. 83: 2 → 0
Char. 86: 1 → 0
Char. 90: 0 → 1
Char. 154: 0 → 2
Char. 170: 0 → 1
Char. 205: 0 → 2
Char. 206: 0 → 1
Node 169:
Char. 68: 0 → 1
Char. 77: 0 → 1
Char. 103: 0 → 1
Char. 142: 0 → 1
Char. 143: 0 → 1
Char. 152: 0 → 1
Char. 210: 0 → 1
Char. 211: 0 → 1
Char. 225: 0 → 1
Node 170:
Char. 114: 0 → 1
Char. 164: 1 → 2
Node 171:
Char. 101: 0 → 1
Char. 198: 0 → 1
Char. 199: 0 → 1
Node 172:
Char. 191: 0 → 1

Char. 194: 0 → 1
Char. 203: 0 → 3
Node 173:
Char. 11: 0 → 1
Char. 20: 0 → 2
Char. 23: 1 → 0
Char. 40: 1 → 0
Char. 151: 0 → 1
Char. 212: 0 → 1
Char. 214: 0 → 1
Char. 267: 0 → 1
Node 174:
Char. 28: 1 → 0
Char. 80: 0 → 1
Char. 82: 0 → 1
Char. 215: 0 → 1
Char. 220: 0 → 1
Node 175:
Char. 217: 0 → 1
Char. 220: 1 → 2
Node 176:
Char. 31: 0 → 1
Char. 203: 0 → 2
Char. 299: 0 → 1
Char. 264: 1 → 0
Node 177:
Char. 28: 0 → 1
Char. 265: 0 → 2
Node 178:
Char. 151: 1 → 2
Node 179:
Char. 91: 1 → 0
Char. 126: 0 → 1
Char. 210: 0 → 1
Node 180:
Char. 253: 0 → 1
Char. 254: 0 → 1
Char. 260: 0 → 1
Char. 267: 0 → 1
Node 181:
Char. 261: 0 → 1
Char. 299: 0 → 1
Char. 342: 0 →1
Char. 355: 0 → 1
Char. 357: 0 → 1
Node 182:
Char. 252: 1 → 0

APPENDIX 5
INSTITUTION LIST

AMNH-FARB	American Museum of Natural History, New York Collection of fossil reptiles, amphibians and birds
BMNH	Natural History Museum, London, UK
BPM	Beipiao Paleontological Museum, Liaoning province, China
BYU VP	Brigham Young University, Provo, Utah
CEUM	College of Eastern Utah, Price, Utah
EME	Transylvanian Museum Society, Department of Natural Sciences, Cluj-Napoca, Romania
FGGUB	Faculty of Geology and Geophysics, University of Bucharest, Romania
FMNH	Field Museum of Natural History, Chicago, Illinois
IGM	Mongolian Institute of Geology, Ulaan Bataar, Mongolia
IVPP	Institute of Vertebrate Paleontology and Paleoanthropology, Beijing, China
JME	Jura Museum, Eichstätt, Germany
GMV	National Geological Museum of China, Beijing, China
MACN	Museo Argentino de Ciencias Naturales, Buenos Aires, Argentina
MCF	Museo Carmen Funes, Plaza Huincul, Neuquén Province, Argentina
MDE	Musée des Dinosaures, Espéraza, France
MIWG	Museum of the Isle Wight Geology, Sandown, Isle of Wight, UK

APPENDIX 5
(Continued)

MML	Museo Municipal de Lamarque, Rio Negro, Argentina
MNHN	Muséum National d'Histoire Naturelle, Paris, France
MOR	Museum of the Rockies, Bozeman, Montana
MOZ	Museo Profesor J. Olsacher, Zapala, Argentina
MPCA	Museo Carlos Ameghino, Cipolletti, Río Negro Province, Argentina
NGMC	National Geological Museum of China, Beijing, China
PIN	Paleontological Institute Moscow, Russia
OMNH	Oklahoma Museum of Natural History, Norman, Oklahoma
SMP	The State Museum of Pennsylvania, Harrisburg, Pennsylvania
TMP	Royal Tyrell Museum of Paleontology, Alberta, Canada
UA	University of Antananarivo, Madagascar
UMNH	Utah Museum of Natural History, Salt Lake City, Utah
WDC	Wyoming Dinosaur Center, Thermopolis, Wyoming
YPM	Yale Peabody Museum, New Haven, Connecticut
ZPAL	Instytut Paleobiologii PAN, Warszawa, Poland

APPENDIX 6

Abbreviation List

Upper case L and R as a prefix signifies left and right.

aa	ascending process of astragalus
al	alveolus
aof	antorbital fenestra
aofs	antorbital fossa
ar	articular
as	astragalus
ax	anterior excavation
bf	brevis fossa
bprd	bifurcated posterior ramus of dentary
brs	brevis shelf
ca	calcaneum
cc	cnemial crest
cf	coracoid foramen
ch	chevron
cmpr	columnlike margin of pterygoid process of quadrate
CN VII	facial foramen
CN X	vagus foramen
CN XI	accessory foramen
CN XII	hypoglossal foramen
ct	coracoid tuber
d	dentary
da	diastema
dg	dental groove
ddp	posterodorsal process of ischium
dtr	dorsal tympanic recess
en	external naris
fc	fibular crest
fh	femoral head
fi	fibula
f.l	lacimal facet
fm	foramen magnum
f.po	postorbital facet
gtr	greater trochanter
j.prqr	junction of palatine and quad rate ramus of pterygoid
lc	lateral crest
ld	ledge below posterior tympanic recess
lr	lateral ridge
mco	medial condyle
mcv	middle cerebral vein
mf	mandibular fenestra
mof	metotic fissure
mos	metotic strut
mt	metatarsal
mx	maxilla
mxar	ascending ramus of maxilla
mxf	maxillary fenestra
mxpp	premaxillary process of maxilla
mxs	maxillary shelf
n	nasal
obr	oblique ridge
oc	occipital condyle
pat	posterior antitrochanter
pf	pneumatic foramen, or popliteal fossa
ph	phalanx
pm	pitted surface of maxilla
pmf	promaxillary foramen
pmx	premaxilla
pneu	pneumatic fossae
pop	paroccipital process
pp	parapophysis
prp	palatine ramus of pterygoid
prz	prezygapophysis
pt	pterygoid, or posterior trochanter
ptr	posterior tympanic recess
q	quadrate
q.pr	contact surface on prootic for quadrate
sa	surangular
sp	splenial
stg	stapedial groove
tbp	tubercle on midshaft of pubis
ti	tibia
tl	tectal lobe
ts	trochanteric shelf
v.o	occipital vein track